

PLANT DISTRIBUTIONS AND COMPETITIVE INTERACTIONS ALONG A
GRADIENT OF TIDAL FRESHWATER AND BRACKISH MARSHES

By

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By

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Plant species distributions and their relation to environmental factors, morphology, competition and disturbance were examined across a gradient of tidal freshwater, oligohaline, and mesohaline marshes along the lower Savannah River. Salinity was significant in separating major vegetation classes between sites, while elevation and distance from tidal channel were significant in separating classes within sites. Overlap among vegetation classes was high, a result of overlap with Scirpus validus, which occurred over the widest range of environmental parameters.

Spatial pattern and relative importance of Scirpus, as well as composition of co-occurring species, changed significantly with changing salinity. Patterns were clumped in the mesohaline marsh, uniform in the strongly oligohaline

marsh, and nearly random at freshwater and oligohaline sites. Field and greenhouse experiments indicated more robust Scirpus under freshwater conditions in the greenhouse, while this trend was reversed at field sites. Transplants of Scirpus between sites had morphologies similar to local populations. Results indicate that morphologic variation in Scirpus is ecophenic and that competition, possibly for light, may be more important in its distribution than environmental factors.

Nested transplants of Scirpus (target species) and neighbor species were combined with species removals in transplants. Neighbor and target species were also transplanted between sites to examine competitive interactions among species. Greenhouse experiments were conducted for species at different densities and salinities. Lastly, feral hog disturbances were documented to determine the possible effects of disturbance.

Results indicate that effects of competitive interactions on plant distributions are not exclusively related to the individual competitive abilities of plant species, but instead reflect a competitive balance of the species involved. Although freshwater marsh species have greater competitive abilities than species of brackish marshes, changes in environmental conditions strongly influence species interactions. While the competitive ability of a weaker competitor itself is not altered,

differences in co-occurring species and environmental conditions result in altered competitive hierarchies and species distributions along an environmental gradient. In addition to environmental gradients, disturbance also appears to alter species interactions and distributions.

CHAPTER 1 GENERAL INTRODUCTION

Overview

The research findings presented in this dissertation are organized into 4 main chapters. Introductory and summary chapters are also included. The introductory chapter includes a literature review of Southeastern freshwater tidal marsh structure and function, a brief description of external factors affecting the system, and project objectives. Chapter 2 provides a descriptive and quantitative analysis of the marsh vegetation and relationships with associated environmental parameters. In chapters 3 and 4, the population dynamics of the only cosmopolitan species occurring in the study area, Scirpus validus, are investigated in regards to its distribution, changing morphology, and relation to co-occurring species across a salinity gradient. Research findings from chapters 2, 3, and 4 culminate in chapter 5, which provides a quantitative analysis of the role of species interactions in structuring these plant communities. The final chapter contains a summary of chapters 2 through 5, with emphasis placed on results and implications from chapter 5.

The System: Freshwater Tidal Marshes

Tidal freshwater marshes, in contrast with coastal salt marshes and inland freshwater marshes, have been studied relatively little (Odum 1988, Odum et al. 1984, Simpson et al. 1983). Unlike inland, non-tidal marshes, they receive high nutrient and energy pulses characteristic of coastal salt marshes. Salinity, the dominant factor affecting the productivity and species richness of salt marshes, is not imposed upon tidal freshwater marshes. As a result, tidal freshwater marshes support a high diversity of plants and animals (Odum 1988, White 1985, Doumlele 1981, Gosselink et al. 1978, Tiner 1977), are extremely productive (Odum 1988, Simpson et al. 1983), and are often sensitive to human impact (Odum et al. 1984, Mitsch and Gosselink 1986).

Tidal freshwater marshes along the South Atlantic Coast make up a significant portion of tidal marshes of the U.S. Coastline morphology of Georgia and South Carolina funnel and amplify tidal waters, creating tides ranging in amplitude from 2.0 to 2.5 meters (de la Cruz 1981), greater than most North American marshes. Unlike geologically younger Pacific coast marshes, there has been time for extensive development over the broad, gently sloping Coastal Plains. In addition, the network of rivers feeding the southeastern marsh system is larger than that of the northeastern tidal marshes that occur over less erodable glacial till. Consequently, deposition of river sediments

into south Atlantic coast marshes is greater than those of northeastern marshes.

Environmental Influences

Tidal freshwater and salt marshes are the extremes of a gradient that includes oligohaline (0.5 - 5 ppt) and mesohaline (5 - 30 ppt) marshes and comprise a gradient that coincides with increasing salinities toward the ocean.

Differences in river and tidal influence are associated with physical gradients of hydroperiod, salinity and soil characteristics and are reflected in distributions of marsh species. These physical parameters are generally considered the primary factors affecting zonation of marsh vegetation (Cooper 1982), though recent evidence indicates species interactions are important in salt marsh vegetation zonation.

Salinity exerts a major influence on tidal marsh habitats (White 1985, Morris 1978, Parrondo et al., Reid and Wood 1976, Phleger 1971, Adams 1963) and appears to be the primary factor in modifying the physical and biological makeup of the transition zone between brackish and fresh water (Odum 1988, Haramis and Carter 1983). High salinities inhibit all but a few halophytes (Phleger 1971) and are associated with decreased species diversity (White 1983, Anderson et al. 1968).

Freshwater marsh communities exhibit relatively little species zonation compared to salt marshes (Odum 1988, Joyce

and Thayer 1986, Carey et al. 1981). Vegetation patterns (White 1985, Leiffers 1983, De la Cruz 1978, Disraeli and Fonda 1978), species diversity (Heinselman 1970) and species ranges (Ferren and Schuler 1980) are, however, strongly influenced by hydrologic regime and site elevation, and elevation is probably the most agreed upon factor influencing marsh zonation (Dawe and White 1982). Major components associated with hydrologic regime include water, nutrients, toxins, oxygen availability and spatial heterogeneity (Gosselink and Turner 1978). Wave exposure (Wilson and Keddy 1986) and current velocity (Nilsson 1987) affect plant diversity as well as plant biomass and vegetative expansion.

Soil Characteristics

Soil characteristics appear less variable than salinity and hydroperiod in tidal marshes. Most North American saltmarshes are formed from reworked marine sediments on marine-dominated coasts (Mitsch and Gosselink 1986), although sediments of both tidal freshwater and salt marshes are of riverine and tidal input. Freshwater tidal marshes are primarily fine textured silts and clays with an organic content ranging from 10-15% in actively flooded levees to 30-45% in high marshes with minimal tidal influence (Simpson et al. 1983). Differences in flood velocity due to levee vegetation also result in the trapping of courser sediments along creek banks (Kirby and Gosselink 1976) and a decrease

in soil redox (Rowell et al. 1981). Organic content of creek levees is lower than high or back marsh soils farther from the creeks. While tidal flushing may be responsible for the rapid litter loss of up to 80% over 30 days, varying rates of decomposition in plant species may be due more to inherent differences in species structure and decomposition rates than tidal influence (Simpson et al. 1983).

Marsh vegetation is significantly affected by changes in soil and interstitial water chemistry under flooded conditions (Ponnamperuma 1972). Except for a thin surface layer, tidal marsh soils are anaerobic due to the slowed diffusion of oxygen through water. The oxygen deficit results in slower organic decomposition and changes in pH, redox, microbial activity, phosphorous, nitrogen and sulfur, as well as metals. The cation exchange capacity and pH increase in acid soils under saturated conditions, while both cation exchange capacity and pH decrease in alkaline soils (Ponnamperuma 1972), resulting in nearly neutral soil pH. An accumulation of toxic metals or solubilization and absorption of high concentrations of micronutrients may also occur under reduced conditions. Sediment nitrogen is bound in an organic form in marshes and is often the primary limiting nutrient for salt marsh plants (Valiela et al. 1978). Phosphorous, however, is often more available to plants of saturated or poorly drained soils. Because iron and aluminum phosphates are more readily reduced, providing

oxygen for the limited decomposition which takes place in these soils, the phosphorous is released and is seldom limiting.

Species Interactions

In addition to environmental factors, differences in distributions among marsh species have been attributed to species interactions (Bertness and Ellison 1987, Snow and Vince 1984) and variation in competitive abilities across an environmental gradient (Wilson and Keddy 1986, Grace and Wetzel 1981). Competition among and between species of terrestrial habitats is well documented, although little experimental data exist for competition among marsh species. While plant zonation has been highly correlated with physical factors such as elevation and salinity, these correlations are not necessarily causal. In addition, physical and chemical gradients associated with marsh vegetation are often obscured by the circular zonation due at least in part to the clonal nature of perennial species.

Salt-tolerant species, e.g. S. alterniflora seedlings (Mooring et al. 1971), S. foliosa (Phleger 1971) and Salicornia bigelovii (Webb 1966), are known to grow well, and in most instances, better, in freshwater. The same species, however, are outcompeted under freshwater conditions, and so are confined to brackish and salt marshes where freshwater species cannot survive (Wainwright 1984). Results of transplant experiments (Wilson and Keddy 1985,

Snow and Vince 1984, Barbour 1978) provide evidence that physiological response of plants to environmental gradients alone does not account for the zonation and patterns characteristic of marsh vegetation. Both interspecific competition and physical disturbance have been found to affect spatial patterns among salt marsh species (Bertness and Ellison 1987).

Results from several studies (Snow and Vince 1984, Grace and Wetzel 1981, Sharitz and McCormick 1980) suggest that along an environmental gradient, competitive interactions may determine species distributions at one end of the gradient, while physiological tolerance limits species distributions at the other. Greater development of "competitive heirarchies" (Anderson 1986) would be expected in freshwater marshes, then, based on the relatively benign environment and greater probability of interactions among species. A random distribution of individuals would ultimately result if there was a total lack of response by individuals to environmental factors or other individuals (Taylor et al. 1978).

Tidal Marshes of the Lower Savannah River

The Savannah River rises on the southern slope of the Blue Ridge Mountains in North Carolina and flows through the Coastal Plain. It is an alluvial, rock-dominated river (as opposed to precipitation-dominated) with a relatively high mineral load derived from weathering and leaching of parent

material in the mountains and Piedmont (Wharton et al. 1982). The Chattooga and Tallulah Rivers form the headwaters of the Savannah River in the Blue Ridge sector of northeast Georgia (Wharton 1978). Rivers originating in the Piedmont generally have larger drainage basins and, because they rise in the mountains where rainfall is heavier, have larger discharges than Coastal Plain rivers (Rhodes 1949). The lower portion of the Savannah River is a deltaic plain. The river discharges through the delta into the ocean via numerous, relatively shallow, interconnected distributary channels between which are scattered marsh islands of various sizes (Rhodes 1949).

The head of the Savannah River tidewaters is about 50 miles north of its mouth. Distributary channels of the delta include: the Little Back, Middle, Back, and Front Rivers (see Chapter 2 for map). The hydrology of the lower Savannah River is dependent upon precipitation, run-off, channel morphology, wind, river discharge, variation in mean sea level, and seasonal and daily tidal fluctuations.

Importantly, 28 percent of tidal freshwater wetlands of the eastern U.S. are found in Georgia and South Carolina. In the lower portion of the Savannah River, approximately 1900 ha, or 21% of the tidal freshwater wetlands in Georgia and South Carolina are found on the Savannah National Wildlife Refuge (SNWR), in addition to bottomland hardwoods, upland forest and artificial impoundments. Artificial

impoundments, left from extensive rice cultivation during the 18th and 19th century (Baden 1975), make up more than 15% of the the total area of South Carolina and Georgia coastal marshes. Former rice fields are evidenced in extensive canal systems traversing much of coastal South Carolina and Georgia, and are especially notable on the lower Savannah River. Vegetation zonation associated with former canal systems is conspicuous. Present vegetation composition is generally consistent with non-cultivated, naturally occurring tidal marshes of the southeastern coast (Odum et al. 1984). Marshes along the lower Savannah River range from fresh to brackish salinities, commensurate with changes in soil, hydrology and plant communities.

The Savannah River Tide Gate

The tide gate is a navigational structure designed to constrict ebbing flows of the Lower Savannah River to the Savannah Harbor channel. In operation, the structure serves as a flap gate and is closed on outgoing tides. Subsequently, flood waters are diverted through connecting lateral channels to the harbor channel of the Front River. Because of the increased flow velocities on ebbing tides the channel is scoured and maintenance dredging in the port is minimized. Like the Mississippi River deltaic plain (Pezeshki 1987), man-made alterations appear to be effecting changes in salinities and hydroperiod, with the potential to significantly alter plant populations and habitat.

The construction of a tide gate at the mouth of the north channel of the Savannah River in 1977 has resulted in increased salinities throughout the refuge (Odum et al. 1977, Pearlstine et al. 1989), and refuge vegetation has undergone significant alterations (Brown et al. 1987). The extent of the salinity wedge upstream, a function of both current and elevation, is farther with the tidegate in operation (Odum 1977, Pearlstine et al. 1989). The wedge extended upstream to the confluence of the Front and Back Rivers in 1943 (USCOE) and 1977 (Odum 1977), and just upstream from Highway 17-A on the Back River in 1977 (Odum 1977) (Fig. 2-1). Since construction of the tide gate, the wedge now 2 - 3 miles farther upstream (Pearlstine et al. 1989). As a result of 15 years of tide gate operations, the lower Savannah River has undergone a conversion from freshwater marsh to a compressed gradient of freshwater and brackish marshes, providing a unique opportunity to document vegetation response to these changes.

Objectives

This objectives of this study were to 1) characterize the vegetation features and environmental parameters of the lower Savannah River tidal marshes; 2) quantify the relationships among vegetation associations and major environmental gradients of salinity, hydroperiod, and soil characteristics; 3) quantify the population dynamics of Scirpus validus in relation to

environmental gradients and co-occurring species; and 4) quantify the effect of species interactions as causal mechanisms for observed plant species distributions and associations.

For objectives 1) and 2), major physical parameters associated with vegetation types were identified and quantified, and correlations among measures of plant species importance and environmental parameters were used to characterize plant species distributions in relation to environmental gradients of salinity, hydroperiod and soil variation in tidal freshwater and brackish marshes. The remaining objectives entailed an investigation into causal mechanisms for species distributions identified in the gradient analysis. Possible reasons for differences in spatial patterns of species distributions in fresh and brackish marsh and development of competitive heirarchies were experimentally determined. Transplant experiments allowed determinations of species robustness, not only in relation to physical and chemical parameters, but also in regards to other species that occupy the same or overlapping niches.

CHAPTER 2
SPECIES ASSOCIATION CHANGES ACROSS A GRADIENT OF
FRESH, OLIGOHALINE, AND MESOHALINE TIDAL MARSHES
ALONG THE LOWER SAVANNAH RIVER

Introduction

Contrast in vegetation, animals, and water and soil chemistry among tidal freshwater and saline marshes is well documented. Differences in river and tidal influence are associated with physical gradients of hydroperiod, salinity and soil characteristics and are reflected in distributions of marsh species. These physical parameters are generally considered the primary factors affecting zonation of marsh plants (Cooper 1982). Salinity exerts a major influence on tidal marsh habitats (White 1983, Morris 1978, Parrondo et al. 1978, Reid and Wood 1976, Phleger 1971, Adams 1963) and may be the principal factor in modifying the physical and biological makeup of the transition zone between brackish and fresh water (Odum 1988, Haramis and Carter 1983). In addition, increasing salinities inhibit all but a few halophytes (Phleger 1971) and result in a characteristically low species diversity (White 1983, Anderson 1986) in saline marshes when compared with freshwater marshes.

Freshwater marsh communities exhibit relatively little species zonation compared to salt marshes (Odum 1988, Joyce and Thayer 1986, de la Cruz 1981). Vegetation patterns

(White 1983, Leiffers 1983, De la Cruz 1981, Disraeli and Fonda 1979), species diversity (Heinselman 1970) and species ranges (Ferren and Schuler 1980) are, however, strongly influenced by hydrologic regime and site elevation, and elevation is the most agreed upon factor influencing plant distributions and zonation (Dawe and White 1982). Major components associated with hydrologic regime include water, nutrients, toxins, oxygen availability and spatial heterogeneity (Gosselink and Turner 1978). Wave exposure (Weisner 1987) and current velocity (Nilsson 1987) also affect plant diversity, biomass, and vegetative expansion.

Vegetation differences and how those differences relate to environmental factors across salinity gradient extremes have received little attention (Odum 1988). Southeastern tidal marshes, both freshwater and saline, have received considerable attention on an individual basis, although the gradient between the two remains poorly studied. A system of freshwater (< 0.5 ppt), oligohaline (0.5-5.0 ppt), and mesohaline (5.0-18 ppt) tidal marshes along the lower portion of the Savannah River provided an opportunity to examine differences in vegetation and associated environmental factors across a strong tidal salinity gradient.

Methods

Study Site

The study area covered 1900 ha of Savannah River tidal marsh, in Chatham County, Georgia, and Jasper County, South Carolina, within the boundaries of the Savannah National Wildlife Refuge ($32^{\circ} 10' N.$, $81^{\circ} 08' W.$). Local tides measure 2.0 to 2.5 meters (de la Cruz 1981). Like much of South Carolina's and Georgia's low country, remnant rice fields from the 18th and 19th centuries are abundant throughout the refuge (Baden et al. 1975). Plant zonation associated with canal drainage is conspicuous, although present vegetation composition is consistent with non-cultivated, naturally occurring tidal marshes of the southeastern coast (Odum et al. 1984).

Four sites were chosen that represented tidal freshwater (0 - .5 ppt), oligohaline (.5 - 2.5 ppt), strongly oligohaline (2.5 - 5 ppt), and mesohaline (5 - 10) marsh conditions (Fig. 2-1). Six transects, each with 3 sample points at distances of 20, 70 and 120 m from tidal channels, were located at each site. Sample points ($n = 73$) were also located adjacent to a secondary canal (canals draining into primary canals) and at approximately equal distances between two secondary canals for a total of 18 sample points at each study site. Because of a sharp turn in the primary canal at the oligohaline site, there was no room for an entire transect at the first sample point. Six

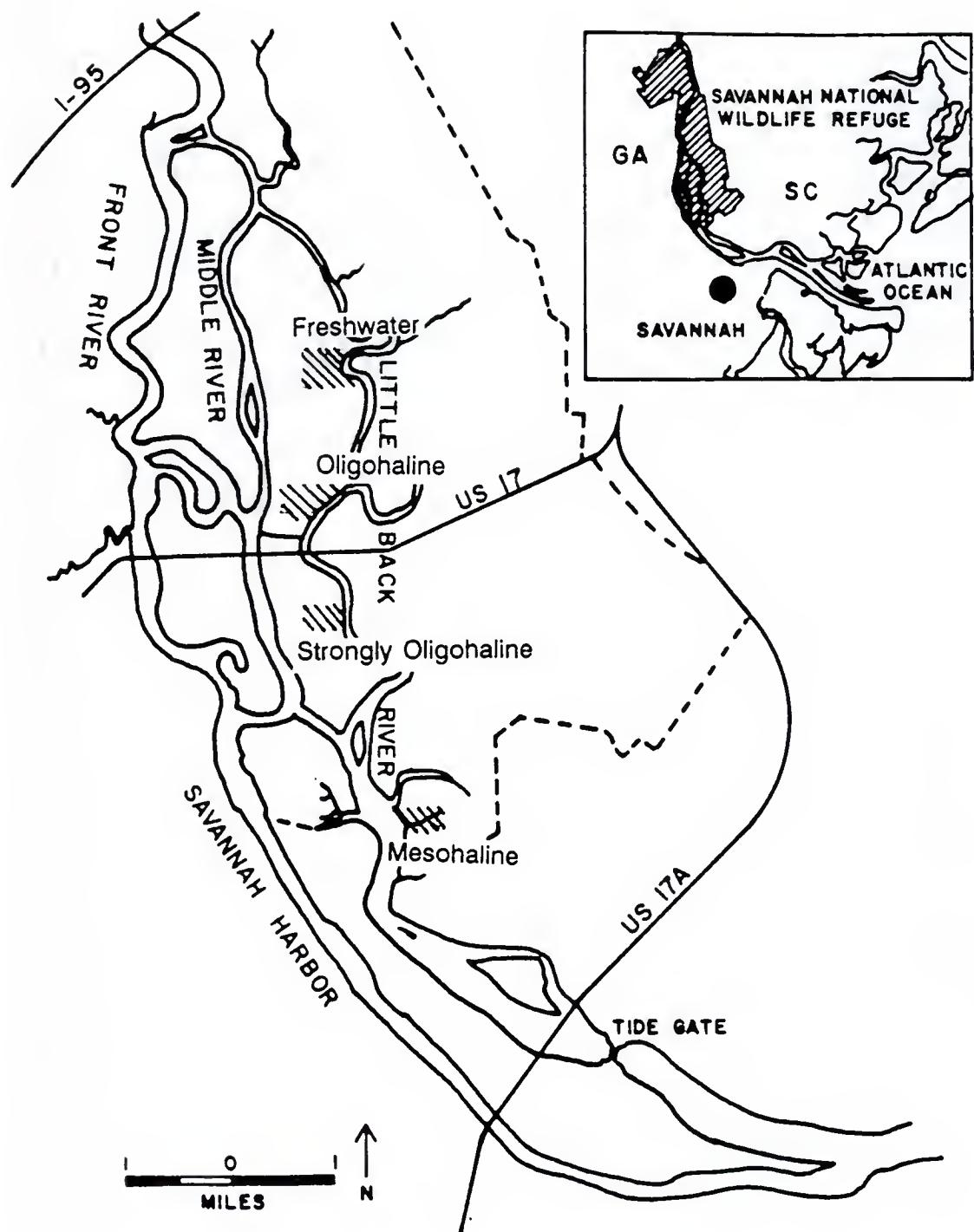


Fig. 2-1. Location of study area along the lower Savannah River, in South Carolina and Georgia. Shaded, numbered areas represent freshwater (1), oligohaline (2), strongly oligohaline (3), and mesohaline (4) sites.

transects were positioned in addition to the first sample point at this site, for a total of 19 points at the oligohaline site, making a total of 73 sample points. Sample points equal distances from primary and secondary canals served as replicates (Fig. 2-2).

Vegetation and Environmental Gradients

Double-nested PVC wells were placed at each sample point. The outer casing was placed 20 cm into the soil to prevent surface water from entering the inner sampling well, and the inner well was placed 30 cm into the soil to collect soil water through vertical slits below the soil surface.

Soil water samples and vegetation were collected at sample points at approximate 8-week intervals from June, 1985, to August, 1987. Surface vegetation was harvested from a randomly placed 0.25 m² circular plot at each sample point during each sampling period. Live vegetation was sorted by species, counted (for a measure of density), dried, and weighed (for a measure of biomass). Absolute densities and biomass were multiplied by four to give density and biomass per square meter for each species. Importance values (IV) were calculated as the sum of relative density and relative biomass for each species in each plot. Dominance-diversity curves, which reflect differences in patterns of competition and niche differentiation in communities (Whittaker 1965) were developed from IV for each species.

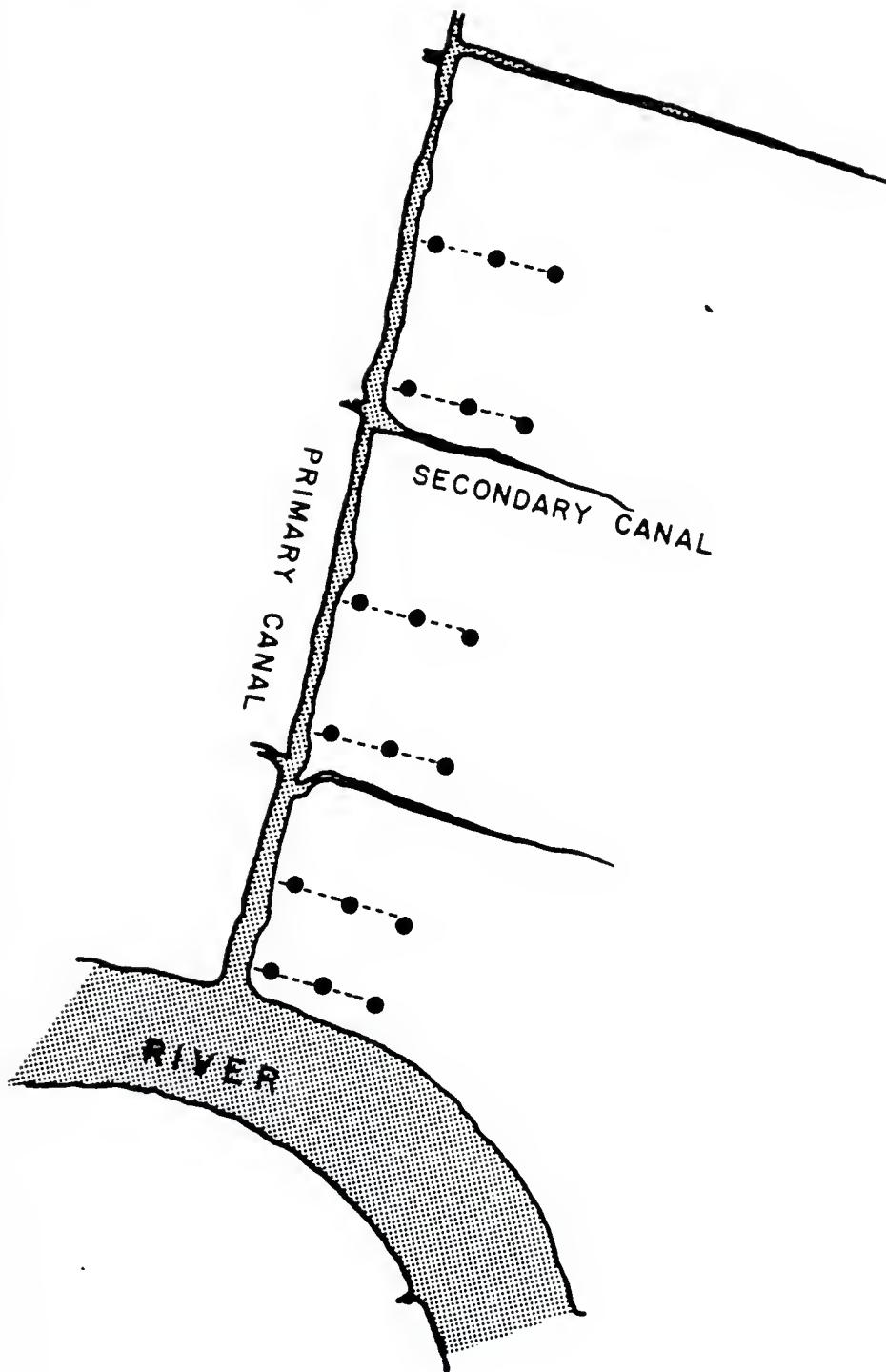


Fig. 2-2. General arrangement of sample points in relation to river and tidal channels.

Interstitial water was siphoned from sampling wells into Nalgene bottles and stored on ice until salinities could be measured from well samples using a Reichert refractometer. Elevations relative to mean sea level were measured with a self-leveling electronic level and verified by permanent benchmarks along the river.

Analysis

Within-site variation in salinity, organic content, and elevation was determined by comparing these variables between low (20 m from channel edge), middle (70 m from channel edge), and high (120 m from channel edge) marsh. Between-site variation in salinity, organic matter and elevation was determined by comparing overall means between sites for each variable. Because the oligohaline site had 1 more point than the other sites, and because there were occasions on which either a sample point was missed or the sample itself inadequately stored, there was not always the same number of samples to compare. Consequently, Tukey's studentized range test for unequal cell sizes was used in means comparisons tests for these variables.

Vegetation classes were chosen based on ordination of species composition at sample points using detrended correspondence analysis (DCA) from the program DECORANA (Hill 1979). DCA is an ordination method which converts species composition data into vegetation variables, which are then assigned scores; vegetation and environmental

patterns can then be compared and used to generate hypotheses about the causes of within-community vegetation patterns (Bernard et al. 1983). Ordination was first applied to all 4 sites combined to examine between-community differences in vegetation. Because of the high diversity of the freshwater marsh, a second ordination of only freshwater and oligohaline sites was done so that within-community vegetation patterns could be examined.

Discriminant function (DF) analysis was then applied to vegetation classes, both for the 4 sites combined and separately. Like multiple regression analysis, DF analysis can be used to predict or describe the relationship between independent and dependent variables. DF analysis was used, however, because the dependent variables in this case, i.e. vegetation classes, are nominal variables, whereas multiple regression analysis relies on interval or ratio variables (Afifi and Clark 1984). DF analysis was used to quantify the contribution of interstitial salinity, elevation, and distance from tidal channels in defining vegetation classes, based on relationships between environmental variables and species composition and dominance at sampling sites. A "successful" DF analysis is one which results in correct pairing of vegetation types and environmental parameters into vegetation classes. Interstitial salinity was used to discriminate between freshwater, oligohaline, strongly oligohaline, and mesohaline sites. Once this first level of

classification was achieved, interstitial salinity, elevation, and distance from tidal channels were used to differentiate among vegetation classes within sites. Environmental variables were retained in the DF analysis based on their significance in predicting vegetation classes at sites. Results were presented as percent correct classifications of vegetation observations.

Results

Differences in soil water salinities (Fig. 2-3) were significant ($P = .01$) between all sites. Average salinities were lowest ($0.54 \text{ ppt} \pm 0.63$) at the freshwater site and increased through oligohaline ($2.10 \pm 1.04 \text{ ppt}$), strongly oligohaline ($4.67 \pm 1.49 \text{ ppt}$) and mesohaline ($9.27 \pm 1.97 \text{ ppt}$) marshes. No sites exhibited significant within-site variation in soil water salinities.

Variation in pH was not significant between sites. Within site variation in pH was also not significant.

Percent soil organic matter (Fig. 2-3) was higher at freshwater and oligohaline marsh sites (43.62 ± 17.2 and 55.28 ± 21.2 , respectively), when compared with strongly oligohaline (38.27 ± 17.3), and mesohaline (31.62 ± 11.7) marsh sites. Differences were significant ($P = .05$) between all except the strongly oligohaline and mesohaline sites. Soil organic matter showed a general increase with distance along transects, i.e. from front to back marsh, at all

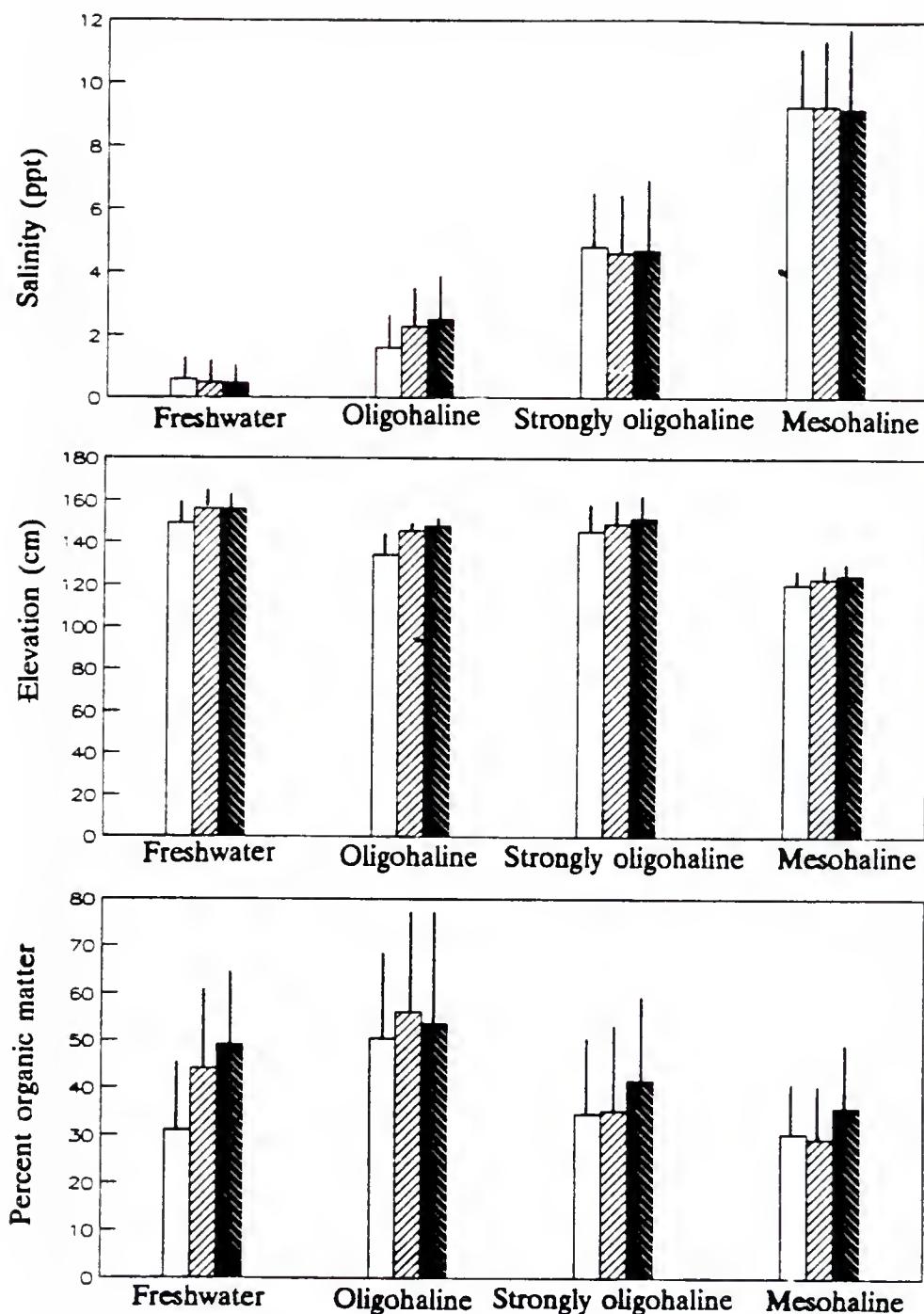


Fig. 2-3. Means and standard deviations for soil water salinities (ppt), percent soil organic matter, and elevation (cm) at 20 (solid bars), 70 (hatched bars), and 120 (open bars) meters from primary creeks at freshwater, oligohaline, strongly oligohaline, and mesohaline sites.

sites. Differences along transects were significant only at freshwater and mesohaline sites ($P = 0.05$).

Mean elevation (Fig. 2-3) was highest at the freshwater and strongly oligohaline sites, lower at the oligohaline, and lowest at the mesohaline site ($F = 42.75$; $n = 18$; $P = .05$). There was an increase in elevation from front to back marsh along transects at all sites, though differences along transects were significant at only the oligohaline site ($F = 9.45$; $n = 18$; $P = .05$).

- On the basis of the DECORANA ordination of the 4 combined sites (Fig. 2-4) and the re-ordination of the freshwater and oligohaline sites (Fig. 2-5), 9 vegetation classes were chosen, the first 6 of which were chosen from freshwater and oligohaline sites: (1) Eleocharis montevidensis, (2) E. montevidensis and S. validus, (3) Zizaniopsis miliacea, S. validus, and Typha latifolia, (4) Z. miliacea, (5) E. montevidensis, S. validus, and Z. miliacea, (6) S. validus and Z. miliacea, (7) S. validus, (8) Spartina alterniflora and S. validus, and (9) S. alterniflora and S. robustus. While overlap between adjacent classes was high, non-neighboring classes did not appear to overlap and the vegetation classes were considered more than adequate. Eleocharis montevidensis was the only dominant species not present in monospecific stands at some point along the salinity or elevation gradients and only S. validus occurred at all sites. The first five

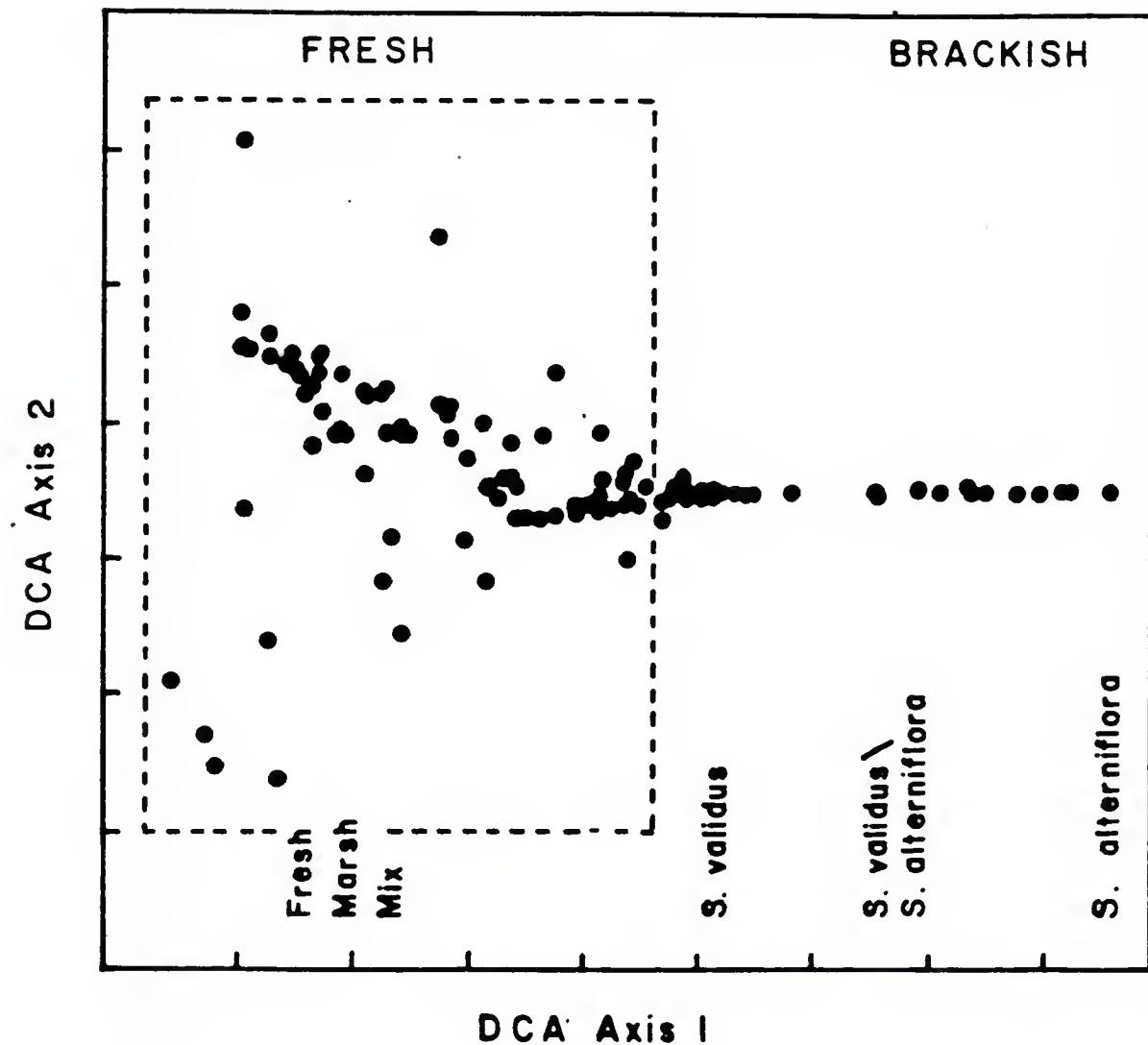


Fig. 2-4. Ordination of sample vegetation scores at freshwater, oligohaline, strongly oligohaline, and mesohaline sites from DECORANA output. Freshwater and oligohaline sample points are contained within the broken line.

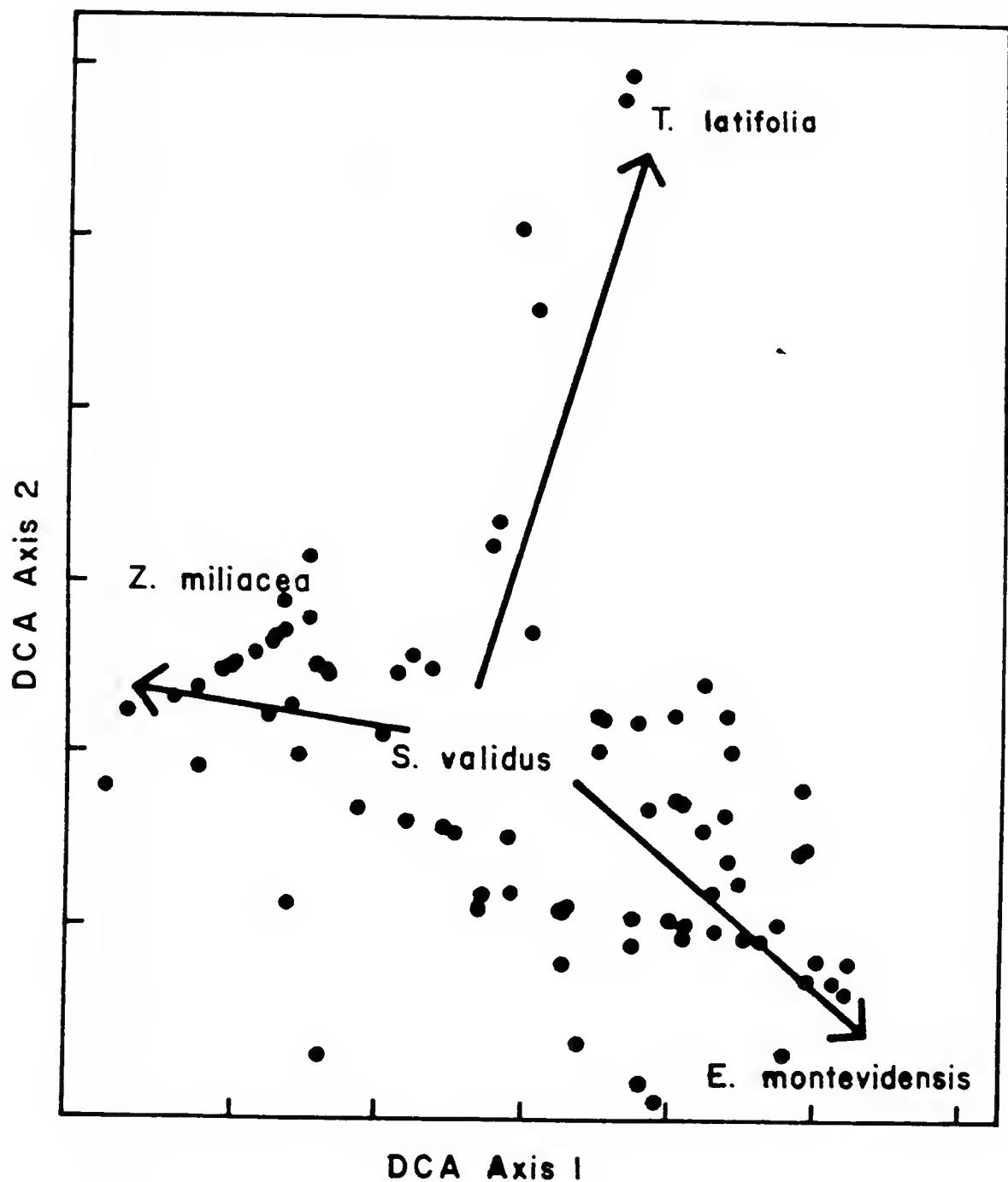


Fig. 2-5. Re-ordinations of sample vegetation scores for freshwater and oligohaline sites from DECORANA output. Arrows indicate decreasing dominance by S. validus and increasing dominance by the species to which the arrow is pointing.

classes included several relatively rare species, including Leersia virginica, Hypericum spp., Mikania scandens, Leersia spp., Aneilema keisak, Aster elliotii, Galium tinctorium, Panicum spp., Sagittaria spp., Polygonum spp., Bidens laevis, Amaranthus cannabinus, and Alternanthera philoxeroides.

Re-ordination of the freshwater and oligohaline sites (Fig. 2-5) shows a separation of freshwater species. The separation of perennials in the freshwater marsh along the first and second axes corresponded to both elevation and distance from tidal channels.

DF analysis for the 4 sites combined (Table 2-1) was highly significant (Wilks-Lambda = 0.05; DF = 24/1529; $P < 0.0$) in classifying (or separating) vegetation classes and more than half of the vegetation classes (60%) were correctly classified. Misclassification (those vegetation classes which were not successfully matched with their corresponding environmental factors) fell almost exclusively into classes containing the same species with different dominants, or different combinations of species with at least one species in common. Interstitial salinity, elevation, and distance from primary channel segregated the majority of vegetation classes. Means for salinity, elevation, and distance from tidal channel were significantly different among vegetation classes ($P = 0.0001$) and as a result were retained in the DF analysis

Table 2-1. Discriminant analysis results of vegetation classes from freshwater (FRESH), oligohaline (OLIGO), strongly oligohaline (S. OLIGO), and mesohaline (MESO) sites on the lower Savannah River. A. Classification matrix. B. Significance of the variable salinity (SAL) in separating vegetation between sites.

A. Wilk's-Lambda = 0.18; F = 1743.28; DF = 3/1144; P = 0.0000.

Class	Percent cases correctly classified			
	FRESH	OLIGO	S. OLIGO	MESO
FRESH	87	13	0	0
OLIGO	37	47	17	0
S. OLIGO	9	13	68	9
MESO	0	2	19	79

B.	Variable	R ²	F	P>F
	SAL	0.82	1743.3	0.0000

(Table 2-1). Interstitial salinity means were significantly different between the four vegetation classes (freshwater marsh, oligohaline marsh, strongly oligohaline marsh, and mesohaline marsh). Percent of vegetation correctly classified by environmental variables was 87%, 47%, 68%, and 79%, for freshwater, oligohaline, strongly oligohaline, and mesohaline sites, respectively.

Within the vegetation classes previously separated by salinity, vegetation was further differentiated into the subclasses by elevation and distances from primary and secondary channels (Tables 2-2 through 2-5). Means for elevation and distances from primary and secondary channels were significantly different among vegetation subclasses for freshwater and mesohaline marsh sites (Tables 2-2 and 2-5). In the oligohaline and strongly oligohaline marsh sites, distance from secondary channels did not contribute to differentiating subclasses; however, means for elevation and distance from primary channels were significantly different (Tables 2-3 and 2-4). In several cases, for example the secondary channels in the freshwater marsh class and channels in the mesohaline marsh class, the correlation coefficient was low and the F score indicates that the variable was significant but a minor contributor to the discrimination. DF analysis was also significant in classifying vegetation within sites (Tables 2-2 through 2-5). Interstitial salinity was not retained as a significant

Table 2-2. Discriminant analysis results of vegetation classes from freshwater sites on the lower Savannah River.
 A. Classification matrix and B. significance values.
 Significant variables were elevation (ELEV), distance to primary channel (CHANNEL), and distance to secondary channel (SECCHAN).

A. Wilk's-Lambda = 0.24; F = 113.26; DF = 9/1260.83; P = 0.0001.

Class	Percent cases correctly classified ^a			
	E	EX	Z	ZX
E	78	0	22	0
EF	17	65	18	0
Z	0	0	66	34
ZX	0	0	0	100

B.	Variable	R ²	F	P>F
ELEV	0.44	136.5	0.0001	
CHANNEL	0.49	168.3	0.0001	
SECCHAN	0.10	19.1	0.0001	

^aE = predominantly E. montevidensis; EX = E. montevidensis mixed with several freshwater annuals, Zizaniopsis miliacea, Scirpus validus, Sagittaria spp., and Hydrocotyle umbellatum; Z = Z. miliacea; ZX = predominantly Z. miliacea, mixed with annuals, E. montevidensis, Scirpus validus, Sagittaria spp., and Hydrocotyle umbellatum.

Table 2-3. Discriminant analysis results of vegetation classes from oligohaline sites on the lower Savannah River.
 A. Classification matrix and B. significance values.
 Significant variables were elevation (ELEV), distance to primary channel (CHANNEL).

A. Wilk's-Lambda = 0.18; F = 1743.28; DF = 3/1144; P = 0.0000.

Class	Percent cases correctly classified			
	FRESH	OLIGO	S. OLIGO	MESO
FRESH	87	13	0	0
OLIGO	37	47	17	0
S. OLIGO	9	13	68	9
MESO	0	2	19	79

B.

Variable	R ²	F	P>F
SAL	0.82	1743.3	0.0000

^aES = predominantly E. montevidensis, mixed with annuals, Zizaniopsis miliacea, Scirpus validus, Sagittaria spp., and Hydrocotyle umbellatum; Z = Z. miliacea; ZX = predominantly Z. miliacea, mixed with annuals, E. montevidensis, S. validus, Sagittaria spp., and Hydrocotyle umbellatum.

Table 2-4. Discriminant analysis results of vegetation classes from strongly oligohaline sites on the lower Savannah River. A. Classification matrix and B. significance values. Significant variables were elevation (ELEV) and distance to primary channel (CHANNEL).

A. Wilk's-Lambda = 0.23; F = 61.50; DF = 6/336; P = 0.0001.

Class	Percent cases correctly classified ^a
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	S	SZ
S	79	21
SZ	14	86

B. Variable R² F P>F

ELEV	0.03	5.28	0.0228
CHANNEL	0.34	84.34	0.0001

^aS = S. validus; SZ = S. validus and Zizaniopsis miliacea.

Table 2-5. Discriminant analysis results of vegetation classes from mesohaline sites on the lower Savannah River. A. Classification matrix and B. significance values. Significant variables were elevation (ELEV), distance to primary channel (CHANNEL), and distance to secondary channel (SECCHAN).

A. Wilk's-Lambda = 0.23; F = 61.50; DF = 6/336; P = 0.0001.

Class	Percent cases correctly classified ^a		
	PR	PS	S

PR	88	0	12
PS	13	67	20
S	0	0	100

B.	Variable	R ²	F	P>F
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ELEV	0.35	46.9	0.0001
CHANNEL	0.03	2.9	0.0578
SECCHAN	0.57	112.72	0.0001

^aPR = Spartina alterniflora and Scirpus robustus; PS = S. alterniflora and S. validus; S = S. validus.

factor in classifying vegetation within sites except at the freshwater site. Elevation and distance to channel were significant in the DF analysis at the freshwater, oligohaline, and mesohaline sites, while only distance to channel was significant at the strongly oligohaline site.

Dominance-diversity curves (Fig. 2-6) are graphs of relative importance (y-variable) as a function of species ranking (x-variable), and represent relative species dominance, or "dominance hierarchies" of a species association. In Fig. 2-6, the strongly oligohaline and mesohaline sites were steeper, with fewer species, and correspond to Whittaker's (1965) geometric curve. Freshwater and oligohaline curves exhibit a more gradual slope and were more similar to lognormal curves characteristic of higher species diversity and more discrete levels within the hierarchies.

Discussion

The vegetation of tidal freshwater, oligohaline, and mesohaline marshes of the lower Savannah River is typical of that described by Baden et al. (1975) for Georgetown County, South Carolina, and for southeastern coastal marshes in general (Odum et al. 1984, Mitsch and Gosselink 1986). Dominant plant species in the tidal freshwater marsh included Z. miliaceae and Polygonum spp. along levees, and Sagittaria spp., Scirpus spp., Typha spp., Eleocharis spp., and several others throughout the low and high marsh.

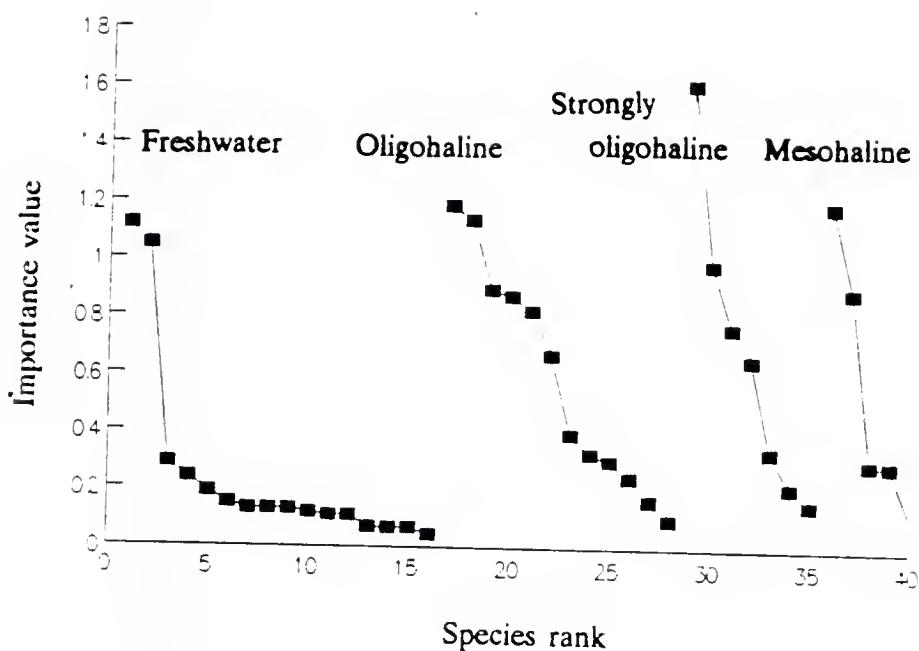


Fig. 2-6. Dominance-diversity curves for species importance values (IV) at tidal freshwater, oligohaline, strongly oligohaline, and mesohaline sites. Each species at each site is represented by a point located by that species' mean IV on the Y-axis, and its position in the sequence of species from highest to lowest IV on the X-axis. IV = relative density + relative biomass.

Dominant species in the more brackish marshes included Spartina cynosuroides, Baccharis halminifolia, and Myrica cerifera along levees, and S. alterniflora, S. validus, and S. robustus in the low and high marsh.

The ordination from DECORANA output successfully separated freshwater from oligohaline and mesohaline vegetation. Ordination of the freshwater site further separated levee (Z. miliaceae), low marsh (S. validus and E. montevidensis mix), and back marsh (S. validus and T. latifolia mix) vegetation. Results emphasized the transition from freshwater species, including Z. miliaceae, E. montevidensis, S. validus, T. latifolia, and annuals, to dominance by S. alterniflora at the mesohaline site.

DCA results suggested the main axis of variation in species composition between the four sites was salinity. These results support several studies (Odum 1988, Ewing 1983, Phleger 1971, Adams 1963) in which salinity was considered the driving force in determining differences in species diversity and plant distributions between tidal freshwater and saltwater marshes. Salinity differences between sites corresponded to changes in species composition, although changes were marked by a gradual transition of species, rather than distinct community types usually evident when comparing freshwater with brackish marshes (Odum 1988). Much of the overlap in vegetation classes along the salinity gradient can be attributed to the

widespread distribution of S. validus. Not only was S. validus a component species of 6 of the 10 vegetation classes, it was also the only species present to tolerate the range of physical factors present over the entire study area. Early successional species have been shown to have broad, overlapping niches in comparison with later successional species, which show greater niche differentiation (Parrish and Bazzaz 1982). The extensive overlap of S. validus with other vegetation classes may reflect its broad fundamental niche, as well as its successional status as an early colonizer that may be displaced.

Continuous overlap in vegetation classes may also reflect a less abrupt salinity gradient (Beals 1969) from freshwater to low salinity marshes. Saltmarshes, in contrast, often have a steep salinity gradient accompanied by distinct plant zonation that coincides with high and low marsh (Phleger 1971, Kruczynski et al. 1978). Steeper environmental gradients place competitors in a smaller area of optimal environment, and interactions among competing individuals may be unavoidable. Over a broader gradient, optimal environment occurs over a larger area and individuals may escape competition just by the availability of more room and less chance for direct contact.

The first DF analysis illustrated between-community differences. The relationship between vegetation classes

and salinity, elevation, and distance from channel was significant, although overlap among vegetation classes was extensive. The second DF illustrated within-community vegetation differences and indicated that elevation and distance from channel were important in classifying vegetation. Elevation largely determines hydroperiod, and subsequent effects of hydroperiod on vegetation composition and distribution are well documented (Mitsch and Gosselink 1986). Although there was a total elevational range of only about 30 cm at each site, low and high marsh are exposed to different flooding regimes, and vegetation zones reflected these differences. The distance from a tidal channel affects the tidal or river current energy reaching different portions of the marsh, the soils deposited in the marsh, as well as the hydroperiod. As a result, distance to channels is also related to plant species richness and community composition (Nilsson 1987). Distance from a tidal channel appeared more important in the distribution of Sagittaria spp. and T. latifolia, for example, which occur predominantly in the back (or high) marsh of the freshwater marsh. Distance from channel may reflect differences in soil consolidation. Because coarser soil materials are filtered out by vegetation, these soils drop out of the flooding water near the levee first, and only very fine silts are transported to the back marsh. Marsh that is not adjacent to tidal channels often has a partially

consolidated surface held together by vegetation (a "quaking marsh"), or even an unconsolidated surface with nearly floating vegetation, which may limit the number of species able to exist in these areas.

Infrequent misclassification of vegetation classes in the DF analysis occurred when a vegetation class overlapped with another in regards to where it occurred in terms of site salinity, elevation, and distance from channel. Classes that overlap share similar habitats based on the measured parameters, and have been shown to occupy the same or similar niches (McNeely 1987). The overlap itself gives no indication of resource preferences of overlapping species, although it does indicate the functional or realized niche of species (Colwell and Futuyma 1971), i.e., what habitat or resource is being exploited. While these results imply overlapping niches among vegetation classes, the extensive overlap most likely demonstrates the similarity in resource requirements and fundamental niche exhibited by most plants (Parrish and Bazzaz 1982, Goldberg and Werner 1983).

Niche width generally decreases as species numbers (McNaughton and Wolf 1970, Pianka 1978) increase and physiological stress decreases (Whittaker 1975, Anderson 1986). This suggests that niche overlap should be least at sites with greater plant species numbers and no salinity stress. Our results seemed at first to contradict this: 41

plant species were identified at the freshwater site where salinities were lowest, compared with 8-12 at each of the oligohaline and mesohaline sites, yet the greatest overlap between vegetation classes occurred at the freshwater site (Table 2-2). The apparent contradiction, however, most likely reflects the steeper environmental gradient of the mesohaline marsh which makes the relationship between vegetation and environmental gradients more discernible.

Importantly, differences in overlap between freshwater and brackish sites also emphasize the problem of measurements of different scale. It has recently been suggested that differences in "hierarchical environmental structure" may explain differences at the community level between severe and relatively benign environments; homogeneity or heterogeneity of a habitat depends on the resolution with which species experience their microhabitats (Kolasa and Strayer 1988, Kolasa 1989). Extensive habitat overlap in the freshwater marsh may indicate a "finer grained" or more homogeneous habitat in which habitat differentiation is not discrete at the level measured, while the steeper environmental gradient of the oligohaline and mesohaline sites exhibit greater differences over the same amount of area and can be considered "coarse grained" habitats (Kolasa 1988). Overlap in vegetation classes is significant only in regards to the environmental parameters measured and the resolution with which they were measured.

Results reflect the scale of measurements made and used in classifying vegetation at each site.

Dominance-diversity curves of species from each site illustrate the contrast in "hierarchical structure" between sites. The geometric curve of the mesohaline and strongly oligohaline marshes are characteristic of severe environments with small numbers of species (Whittaker 1975). Here, dominance is strongly developed and niche space is not evenly divided among several species. Species dominance in the freshwater and oligohaline marsh correspond more closely to a lognormal distribution (Preston 1948) and is determined by several factors that affect the competitive success of species relative to one another. Species rich communities and communities in which species occur across a wide environmental range approach such lognormal distribution. These curves represent freshwater plant species distributions across benign environmental gradients which exhibit only slight changes in regulating factors, thus many plants compete equally for resources. In contrast, steep gradients and physiological stress of brackish marshes may result in well-developed dominance among a few species competing for the same resources.

Physical parameters such as hydroperiod, salinity, and soil characteristics have been strongly associated with plant distributions. While these factors may be the dominant factors affecting plant associations in the

Savannah River marshes, competition is often important in structuring plant communities (Bertness and Ellison 1987, Barbour 1978), and it has been suggested that overlap in resource utilization indicates competition among some prairie plants (Platt and Weis 1977). Several studies have shown species may be differentially displaced by competition along an environmental gradient (Barbour 1978, Rabinowitz 1978, Grace and Wetzel 1981, Snow and Vince 1984). Studies with Jaumea carnosa (Barbour 1978), S. alterniflora (Adams 1963), Spartina foliosa (Phleger 1971), and Typha angustifolia (McMillan 1959) have found that these species grow better in freshwater but are confined to higher salinity marshes by species better specialized to freshwater conditions. Competitive interactions may be more important to within-community structure, while salinity and other physical parameters exert a greater influence on between-community structure.

The importance of competition cannot be overlooked in any explanation of plant distributions. While results of the present study are not sufficient to address the role of competition in structuring these plant associations, competition will be addressed in subsequent chapters.

CHAPTER 3
SPATIAL DISTRIBUTIONS OF THE SOFTSTEM BULRUSH,
SCIRPUS VALIDUS, ACROSS A SALINITY GRADIENT

Introduction

Plant species distributions in tidal marshes have been attributed predominantly to environmental gradients of salinity (Phleger 1971, Morris et al. 1978, Leiffers 1983, Haramis and Carter 1983, White 1983), site elevation and hydroperiod (Ferren and Schuler 1980, Lieffers 1983, Dawe and White 1982, White 1983), and soil characteristics (Kirby and Gosselink 1976). In salt marshes, where environmental gradients are often steep and correlated with one another, they may be strongly associated with community structure and species distribution patterns (Snedaker 1982, Hoover 1984). Clumped distribution pattern or zonation of salt marshes may indicate a species response to environmental gradients (Pielou and Routledge 1976, Cooper 1982, Vince and Snow 1984), competition (Snow and Vince 1984, Bertness and Ellison 1987), or physical disturbance (Turner 1987, Bertness and Ellison 1987).

Zonation in tidal freshwater marshes is much less distinct than in salt marshes (Odum 1988). There is greater overlap in habitat (de la Cruz 1981, Joyce and Thayer 1986, Odum 1988), and relations among species and environmental

factors are more complex (Hoover 1984, Odum 1988), obscuring species zonation.

Although the importance of pattern in plant species distributions has received considerable attention (Pielou and Routledge 1976, Mack and Harper 1977, Dale 1986, Shaltout 1987), comparative studies are generally restricted to species distributions within a community type (e.g. salt marsh) and do not address community distribution patterns between community types (e.g. tidal freshwater to salt marshes). Because species interactions occur at the level of individual neighbors (Mack and Harper 1977, Fowler and Antonovics 1981) the distribution patterns of a single species may affect larger scale community structure (Harper 1977, Fowler and Antonovics 1981, Dale 1986).

In this study, the distribution patterns of *Scirpus validus*, a dominant species in both freshwater and brackish marshes along the lower Savannah River, were examined. The objectives were to (1) determine the distribution patterns of *S. validus*, and (2) examine the role of environmental factors in the distribution of *S. validus*.

Methods

Mean number of species at each site and species similarity between sites (Whittaker 1975; $I_s = (\text{total species at site } x \text{ plus the total species at site } y)/\text{number of species common to both sites})$) were calculated.

Between-site differences in environmental variables and species numbers were compared using Waller-Duncan multiple means comparison tests. The same test was used to compare changes in soil organic matter associated with distances from primary creeks along transects. Elevation changes along transects were compared using Tukey's standardized range test.

Coefficients of dispersion (CD) were calculated for each site, for each sampling period, as the variance to mean ratio of standing densities of S. validus. The coefficients were used as a measure of the amount of nonrandom dispersion of stems (see Sokal and Rohlf 1981, Whittaker 1975, Kershaw 1973). A CD value equal to 1 indicates a random distribution of individuals. Clumped distributions have a $CD > 1$, and a $CD < 1$ represents a uniform distribution. Paired t-tests were used to determine departures from randomness (i.e., CD values significantly different from 1). Between-site differences in CD values were compared using Waller-Duncan multiple means comparison tests.

Multiple regression analysis was used to examine the relations of S. validus importance values (IV) with measured environmental parameters at sites (see Methods and Results, Chapter 1). Regression analysis was also used to examine the relationship of species numbers and IV with the salinity gradient across all 4 sites.

Results

Species Associations

The average number of species was significantly greater at the freshwater site ($F = 28.73$; $N=27$; $P = 0.05$). The number of species was not significantly different among the oligohaline, strongly oligohaline, and mesohaline sites. Freshwater marsh had an average of 18 species, compared to less than 7 in the oligohaline, 3 in the strongly oligohaline, and 5 in the mesohaline marsh (Fig. 3-1). The large number of species in the freshwater marsh was due mostly to the presence of annual species. Similarity in species composition was greatest between the strongly oligohaline and mesohaline and least between freshwater and mesohaline marsh sites (Table 3-1).

The highest mean IV for S. validus (Fig. 3-2) occurred in the strongly oligohaline marsh (Mean = 1.16), and the lowest at freshwater (Mean = 0.39) and mesohaline (Mean = 0.41) sites. Scirpus validus was surpassed in IV by Zizaniopsis miliacea and Eleocharis montevidensis at the freshwater site, and by Spartina alterniflora in the mesohaline marsh. Scirpus validus had the highest IVs at oligohaline and strongly oligohaline sites.

Spatial Pattern

Differences in interstitial salinities were accompanied by differences in spatial pattern in S. validus (Fig. 3-3). Coefficients of dispersion (CD) exceeded 1.0 ($P = .05$) at

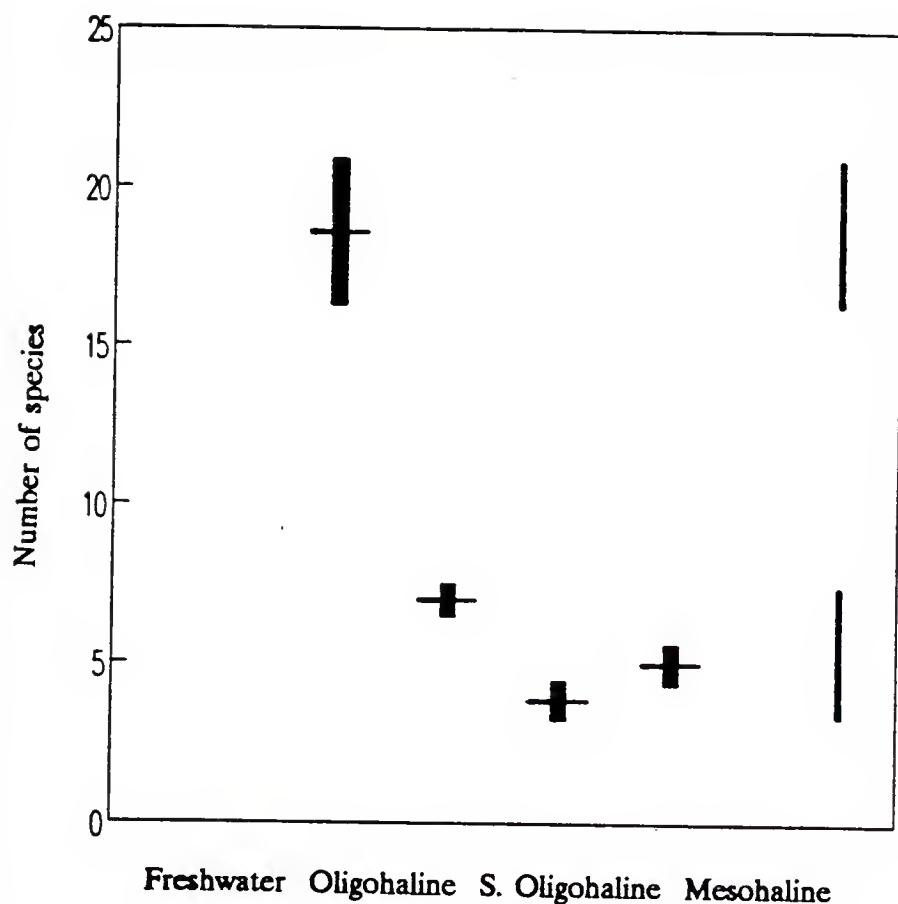


Fig. 3-1. Mean number of species (± 1 standard error) at freshwater, oligohaline, strongly oligohaline (S. Oligohaline), and mesohaline sites. Means falling within the same vertical line to the right of graph are not significantly different (Waller-Duncan, $P = 0.05$).

Table 3-1. Similarity in species composition (I_s) between freshwater, mildly oligohaline, strongly oligohaline, and mesohaline sites.

Site	Fresh	Oligo	S. Oligo	Meso
Fresh	1.00			
Oligo	0.51	1.00		
S. Oligo	0.20	0.43	1.00	
Meso	0.12	0.25	0.71	1.00

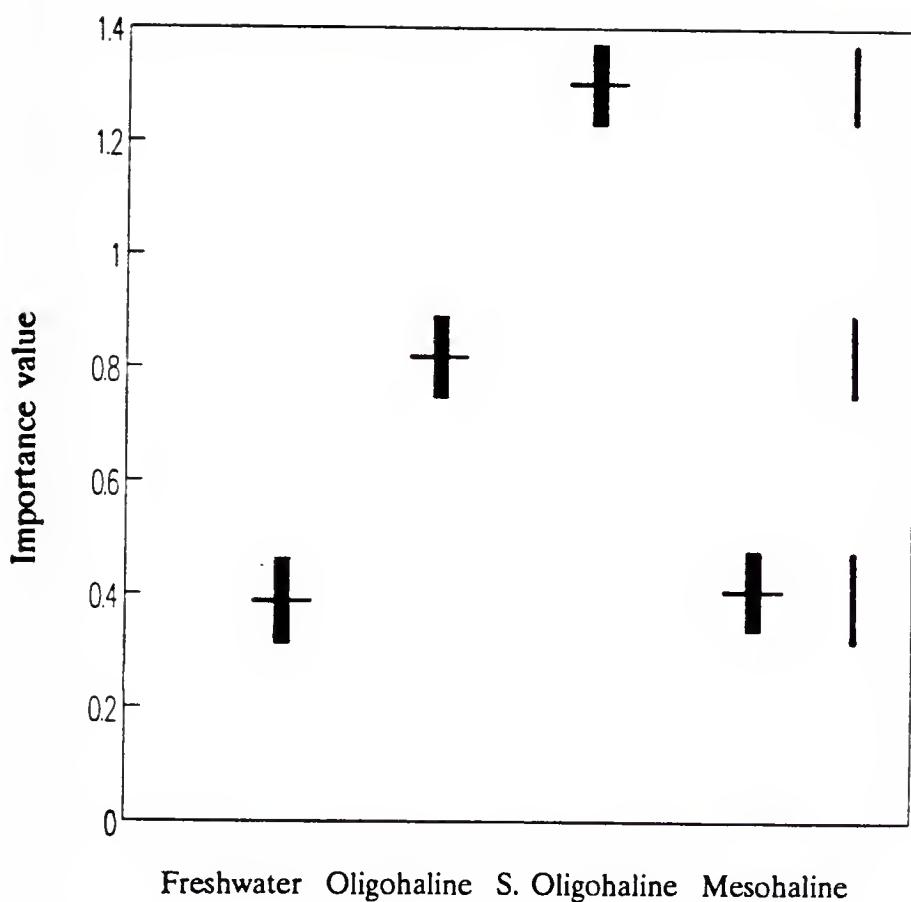


Fig. 3-2. Mean Importance Values (± 1 standard error) for *S. validus* at freshwater, oligohaline, strongly oligohaline (S. Oligohaline), and mesohaline sites. Means falling within the same vertical line to the right of graph are not significantly different (Waller-Duncan, $P = 0.05$).

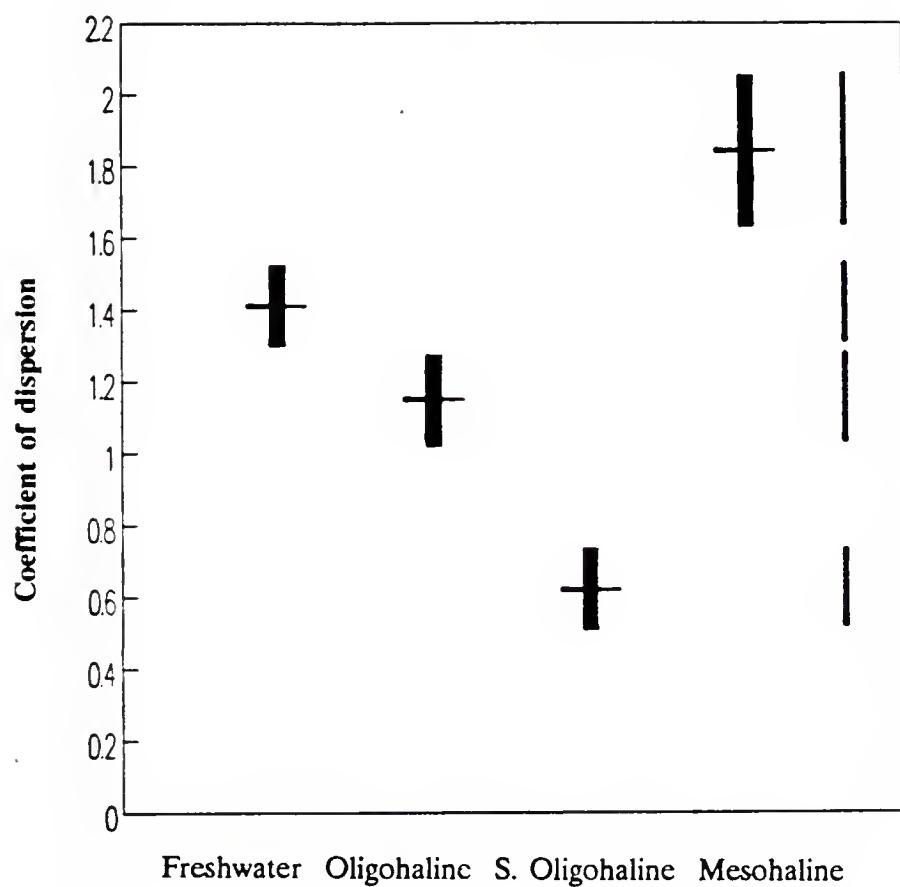


Fig. 3-3. Mean Coefficients of Dispersion (± 1 standard error) for *S. validus* over a gradient of increasing soil water salinities at freshwater, oligohaline, strongly oligohaline (S. Oligohaline), and mesohaline sites. Means falling within the same vertical line to the right of graph are not significantly different (Waller-Duncan, $P = 0.05$).

the freshwater (Mean = 1.41; STD = 0.28; n = 7), and mesohaline (Mean = 1.84; STD = 0.55; n = 7) sites, indicating clumped distributions. CD values of S. validus at the strongly oligohaline site (Mean = 0.62; STD = 0.28; n = 7) were significantly less than 1.0, indicating a uniform distribution of S. validus. Only the oligohaline site (Mean = 1.15; STD = 0.34; n = 7) exhibited a random distribution of S. validus ($P = 0.24$). CD values indicated significantly greater clumping in the mesohaline marsh when compared to the freshwater and oligohaline sites ($F = 12.73$; $P = .05$).

Relationship of IV with Environmental Variables

Importance values for S. validus (Fig. 3-1) showed a significant quadratic relationship with increasing soil water salinities ($y = 0.35 + 0.4x - 0.03x^2$; $R^2 = 0.16$; n = 448; $P = 0.0001$). Scirpus validus IVs were significantly related to soil water salinities and elevation at all but the oligohaline site (Table 3-2). R-square values for multiple regressions were less than 0.30 for all 4 sites. Salinity and elevation added significantly to the regression model in determining S. validus IV at the freshwater site ($P = .05$). Elevation, but not salinity, was significantly related to IV at the mildly oligohaline ($P = .05$) and mesohaline ($P = .05$) sites. Only salinity was significantly related to IV at the strongly oligohaline site ($P = .05$).

Table 3-2. R-square, n, F, and P values for multiple regression analysis of S. validus IVs with interstitial salinities (ppt), elevation (cm) and percent soil organic matter at freshwater, mildly oligohaline, strongly oligohaline, and mesohaline sites.

Site	R ²	N	F
Fresh	0.23	103	4.80**
Oligo	0.13	87	1.96*
S. Oligo	0.25	100	5.23**
Meso	0.27	91	5.11**

*P = 0.05; **P = 0.01

Soil organic content was not significant in determining S. validus IVs at any site.

Discussion

Species Diversity

The decrease in species numbers and replacement by other, more salt tolerant species across the 4 sites were typical of community changes from freshwater to brackish marshes. Species similarity was greatest for those sites with similar salinity regimes and least for those with greatest differences in soil water salinities. Seasonal differences in species composition due to annuals strongly influenced species diversity in freshwater marshes. High species similarity between adjacent sites along the continuum from freshwater to mesohaline marsh, and the overlap of S. validus throughout the gradient emphasize the gradual shift in species composition from freshwater to brackish marsh plant communities in this study.

Distribution Patterns

Coefficients of dispersion indicate a significant change in spatial pattern for S. validus across the salinity gradient. Scirpus validus was clumped in monospecific stands at the mesohaline site. Significantly less clumping occurs in freshwater and very low salinity marshes, where S. validus was interspersed with freshwater plant species. At the strongly oligohaline site, S. validus had a uniform spatial distribution, rather than the discrete clumps found

clumps found in the mesohaline marsh. Species diversity was low and IVs of S. validus high at intermediate salinities.

Uniform and clumped distributions, while not proof of competition or environmental specialization, do indicate that more than random chance is at work in producing or maintaining the pattern. The uniform, or regular, distribution of individuals occurs when available space is almost fully occupied (Pielou 1959), allowing each individual the same amount of space. While changes in pattern among most wetland species have not been examined, some desert shrubs exhibit uniform distributions as a result of intra-specific competition (King and Woodell 1973, Shaltout 1987). Intraspecific competition may explain the distribution of S. validus at the strongly oligohaline site in this study, where freshwater species are physiologically intolerant and Spartina alterniflora is infrequent except at the edges of canals and the river. With few co-occurring species and high densities of S. validus, neighborhood competition among individuals may be limited to competing individuals of S. validus, resulting in a uniform distribution pattern.

Results from several studies (Sharitz and McCormick 1973, Grace and Wetzel 1981, Snow and Vince 1984, Wilson and Keddy 1986) suggest that along an environmental gradient, competitive interactions may determine species distributions at one end of the gradient where tolerance ranges overlap,

while physiological tolerance limits species distributions at the other end of the gradient. Separate multiple regressions of S. validus IV with environmental factors at each site indicate a stronger relationship at the mesohaline site. This suggests that environmental gradients are primarily responsible for the clumping of S. validus at the mesohaline site, where salinities are highest. The clumping pattern reflects dominance of single species in zones, and possibly greater habitat differentiation in the more saline marsh between a limited number of species. Competition, environmental tolerance, disturbance, and vegetative growth, all probably play a role in explaining the clumped distribution of S. validus.

Given the wide environmental tolerances of S. validus and the large number of species at the freshwater site, the distribution pattern at this site may be influenced more strongly by competitive interactions. Resources must be shared with neighboring individuals and individual stems occur much farther apart. Variations in light, created by differences in plant architecture and growth form (Jones 1983), and subsequent competition for light and space, may account for variation in densities of S. validus in the freshwater marsh.

While physiological mechanisms alone do not explain the quadratic relationship of importance values for S. validus with increasing soil water salinities, the relationship may

be explained by a combination of physiological and environmental mechanisms. Scirpus validus is distributed across a broad environmental gradient along the lower Savannah River. A wide range of environmental tolerances has been reported for this wetland plant (Beal 1977, Barko and Smart 1978, Langeland 1981, Barclay and Crawford 1982, Joyce and Thayer 1986), which reproduces readily both vegetatively and by seed (Godfrey and Wooten 1979). Like saltwater and brackish marsh plants that generally grow best in freshwater but are limited by competition (Mooring et al. 1971, Phleger 1971, Barbour 1978), S. validus may also be limited by competition to intermediate salinities where freshwater species cannot survive and extreme salt tolerant species cannot compete well.

The quadratic relationship between IV and salinities also reflects pattern differences among sites. At the strongly oligohaline site, where the CD value was lowest, S. validus exhibited the highest stem densities and occurred with few other species. Salinities at this site appear to be high enough to limit freshwater species without inhibiting S. validus.

Lower IVs in the freshwater site reflect low densities of S. validus mixed with many other species in a clumped distribution, but less clumped than at the mesohaline site. Generally, S. validus occurred in very high densities or not

at all in the mesohaline marsh due to increased species zonation.

Elevation, but not salinity was significantly related to S. validus IVs in mildly oligohaline marsh. Higher salinities extend farther upstream in the Middle River than in the Little Back River. Consequently, interstitial salinities at the mildly oligohaline site reflect higher salinities of the Middle River on the northwest side of the marsh and lower Back River salinities on the southeast side. While variation in salinities was greatest at this site, it was still significantly different from other sites.

Significant changes in spatial distribution along physical gradients for S. validus in this study suggest that salinity strongly influences its distribution, but not directly. Scirpus validus is a generalist species, capable of growing well over a wide range of salinities. Many other species perform as well or better at low salinities and in freshwater, but resources must be shared by all species under these conditions. As salinities increase, less species are physiologically tolerant, and S. validus occurs as a dominant species. As salinities increase across the salinity gradient, Spartina alterniflora and Scirpus robustus are able to better compete for resources, and dominance by S. validus decreases.

Within individual sites, the influence of a salinity gradient appears to be replaced by less distinct elevational

differences, and changes in species distributions also become less distinct. In this study, elevation was a significant factor in determining IVs of S. validus within a site. Low elevations at the mesohaline site resulted in increased hydroperiod which, combined with increased salinities, may account for the increase in dominance by S. alterniflora and zonation of S. validus in the higher marsh.

CHAPTER 4
MORPHOLOGICAL PLASTICITY IN SCIRPUS VALIDUS
ALONG A SALINITY GRADIENT

Introduction

Results of several transplant experiments have demonstrated both ecotypic and ecophenic variation in plant morphology along environmental gradients. After being transplanted to different habitats, morphological characteristics of glasswort (Salicornia europaea) (Ungar 1987, Jefferies 1981), cinquefoils (Potentilla erecta) (Watson and Fyfe 1975), and yarrow (Achillea millefolium) (Clausen et al. 1948), were shown to remain constant, exhibiting ecotypic variation.

Species from contrasting habitats may also have a morphology that changes in response to the environment. In experiments with Spartina alterniflora (Shea et al. 1975), and several other salt marsh species (Seliskar 1985), plants that were moved from one end of a salinity gradient to another became morphologically similar to their new neighbors, exhibiting ecophenic, rather than ecotypic, variation in contrasting habitats.

Salt marshes often exhibit gradients of increasing soil salinities from low to high marsh as a result of less frequent tidal inundation and increased evaporation and

plant evapotranspiration in the high marsh. Decreases in density, biomass, and/or height for Sporobolus virginicus (Donovan and Gallagher 1985), Spartina foliosa (Phleger 1971), Juncus roemerianus and Spartina alterniflora (Kruczynski et al. 1978) have been associated with the increased salinities from low to high marsh in field and greenhouse experiments.

Tidal amplitudes along the lower Savannah River in South Carolina and Georgia range from 2.5 to 3 meters, inundating most of the marsh, and eliminating any salinity gradient from low to high marsh at a given site. Marshes are, however, associated with the first 28 miles of the river from the ocean, and there is a wide salinity gradient downstream to upstream. In this region, Scirpus validus is the only species consistently present throughout tidal freshwater, oligohaline, and mesohaline marshes that otherwise differ strongly in species composition.

The objectives of this study were to test 1) whether morphological variation in S. validus is significant between contrasting habitats, 2) whether morphological variation in S. validus is ecotypic or ecophenic, and 3) whether measured differences in morphology are directly related to salinity. Light extinction was also measured to determine whether it may have a more direct influence than salinity on morphological variation in S. validus. Because different growth morphologies may influence macrophyte community

composition (Barko and Smart 1981), variation in S. validus morphology may further understanding of factors which help structure plant communities in this area.

Methods

The study area included freshwater (0 ppt), oligohaline (5-7 ppt), and mesohaline (9-10 ppt) tidal marshes of the lower Savannah River, in Chatham County, Georgia, and Jasper County, South Carolina. Vegetation composition in the study area is similar to other non-cultivated, naturally occurring tidal marshes of the southeastern coast (Odum et al. 1984, and see Ch. 1 and 2).

In July 1987, S. validus stem densities, internode lengths of rhizomes, and stem heights were measured. Measurements were made on 10 replicate S. validus stems from 10 random, 0.25 m² plots at each site. Variation in S. validus stem heights and internode lengths were calculated using the coefficient of variation, CV = (standard deviation / mean) x 100. CV values indicate the relative amount of variation in stem height and internode length within each site.

In December 1987, S. validus in 0.25 m² plots, approximately 15 cm deep, were randomly collected from the oligohaline marsh site. Twenty of these plots were transplanted to the freshwater site and 20 to the mesohaline site. Five additional plots at the donor site were removed and then replaced as controls to determine if transplanting

effects were significant. Eighteen undisturbed plots previously established at each site were used for comparison with transplants and controls (A Reichert refractometer was used to measure and monitor soil water salinities at field sites and in the greenhouse). Above-ground vegetation from transplants, controls, and undisturbed plots was harvested in June 1989. Stem heights and densities were measured for each plot. Because there was no way to determine which parts of rhizomes were produced during the 1.5 years at transplant sites, internode distances were not measured for transplants.

In December 1988 a total of 60 rhizome sections of S. validus were collected randomly from freshwater, oligohaline, and mesohaline sites. Sections were washed free of soil and debris, cut into node sections 2.5 cm in length, and planted in shallow greenhouse trays of potting soil. Three treatments, each consisting of 2 trays from each site and 10 sections per tray, were watered daily with 0, 5, and 10 ppt seawater solution for 6 months.

Differences in light extinction between sites and between vegetation types were also measured in December 1988. Light intensity ($\mu\text{E} \times \text{m}^2 \times \text{sec}^{-1}$) was measured at the top of the vegetation canopy and at ground level using a LICOR quantum radiometer (Model # LI-185B) and a flat quantum sensor. Light extinction coefficients through the vegetation were calculated from the LICOR measurements.

Three replicate readings were taken at 10 random points within each vegetation type and percent cover of vegetation was recorded at each site. Vegetation types at the mesohaline site were based on dominant species. Vegetation types were S. validus, Spartina alterniflora, and Spartina cynosuroides in the mesohaline marsh. Vegetation types in the freshwater marsh were Eleocharis montevidensis, S. validus mixed with Zizaniopsis miliaceae, and S. validus mixed with Eleocharis montevidensis.

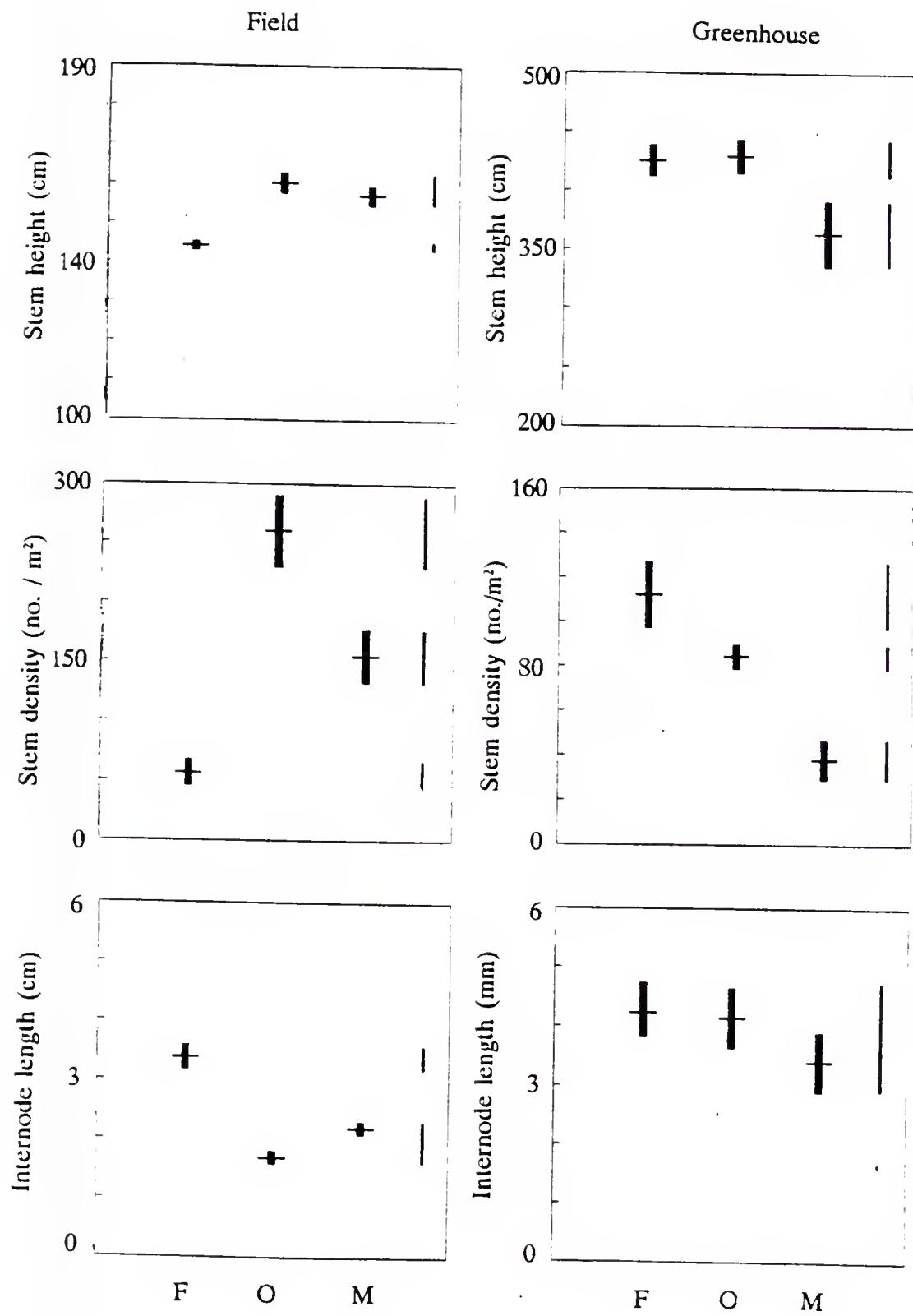
Waller-Duncan multiple means comparison tests ($P = 0.05$) were used to compare greenhouse measurements, field measurements, and light extinction treatments. Means comparisons were also used to determine if differences were significant ($P = 0.05$) between transplanted plots, control plots, and undisturbed plots, within treatments. Student's t-test ($P = 0.05$) was used to compare transplanted densities and stem heights between freshwater and mesohaline sites.

Results

Field Measurements

Scirpus validus had shorter internode lengths, taller stems, and greater densities at the oligohaline and mesohaline sites when compared with the freshwater site (Fig. 4-1). These traits were not significantly different between oligohaline and mesohaline marsh sites, although both differed significantly from the freshwater site. Variation in stem height of S. validus was lowest at the

Fig. 4-1. Mean (\pm 1 SE) internode lengths, stem heights, and stem densities for S. validus from field sites and greenhouse. Means falling within the same vertical line to the right of graph are not significantly different (Waller-Duncan, $P = 0.05$).



freshwater site for stem height ($CV = 6.3$), and higher at the mesohaline ($CV = 10.98$) and oligohaline ($CV = 12.4$) sites. Variation in internode distance was highest at the oligohaline site ($CV = 79.9$), and lower at the freshwater ($CV = 48.4$) and mesohaline ($CV = 46.1$) sites.

Greenhouse Experiments

Stems/m² (and node survival) were greater overall for freshwater treatments (Fig. 4-1). Stem densities and surviving nodes did not differ between freshwater and oligohaline treatments. The oligohaline and mesohaline treatments were not significantly different from one another with respect to stem density. Stem heights of *S. validus* were also significantly greater for freshwater and oligohaline treatments when compared with mesohaline treatments (Fig. 4-1), though stems did not grow to heights measured in the field. Differences in internode lengths between treatments were not significant.

Transplants

Scirpus validus transplanted from the oligohaline site to freshwater and mesohaline sites changed significantly in stem height and density after 18 months. In contrast with greenhouse results, *S. validus* transplanted to higher salinities had taller stems and greater stem densities when compared with freshwater transplants (Fig. 4-2).

Stem heights of *S. validus* transplants from the oligohaline site converged with values characteristic of the site to which they were transplanted (Fig. 4-2). Stems of

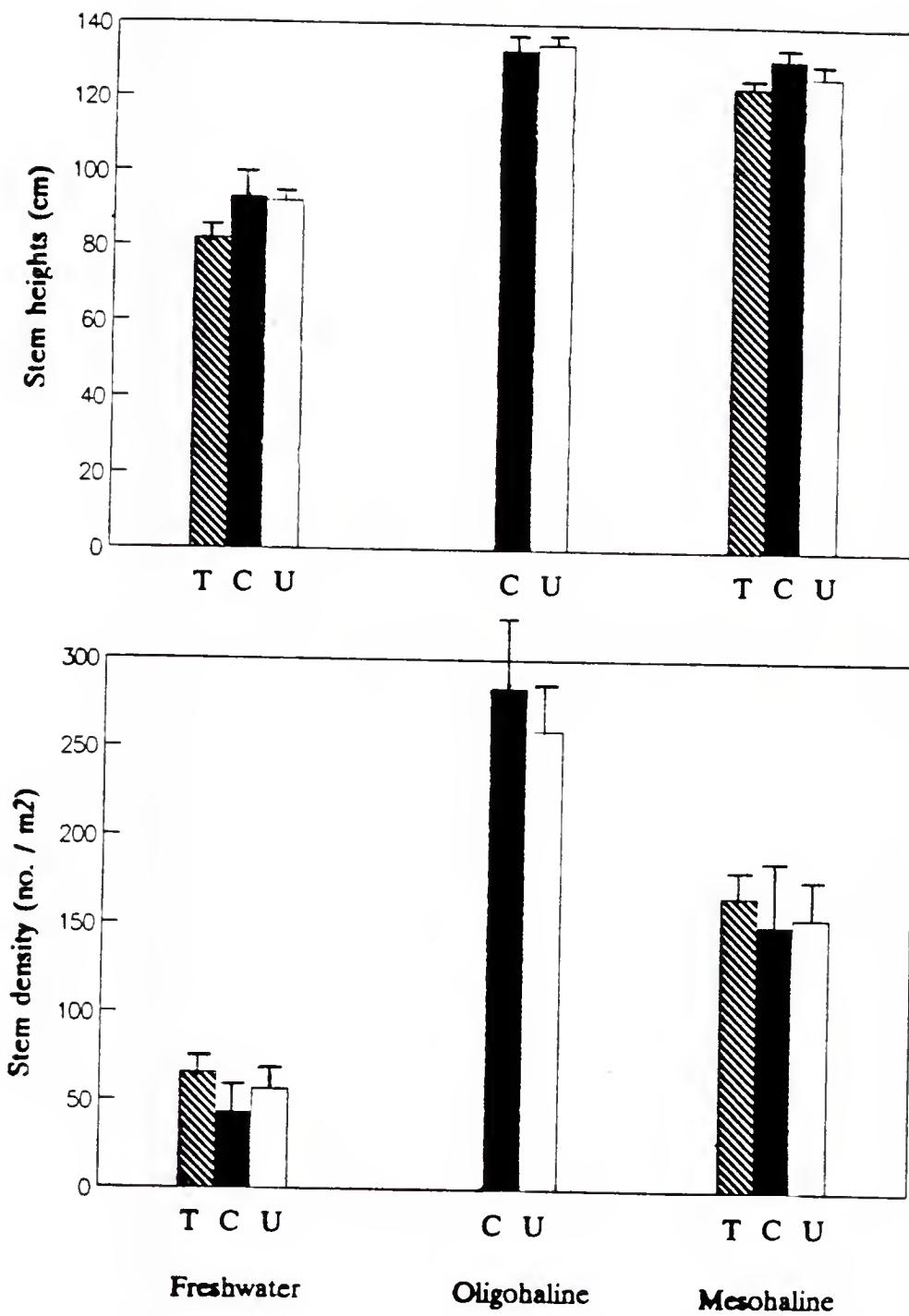


Fig. 4-2. Mean (± 1 SE) stem heights and stem densities for *S. validus* transplanted from oligohaline marsh to tidal freshwater and mesohaline marsh. Hatched bars represent mean values for transplanted plots (T), solid bars represent

transplants were significantly shorter at the freshwater site when compared with the mesohaline site. Differences in stem heights were significant between freshwater transplants and oligohaline control plots, while differences between mesohaline transplants and oligohaline control plots were insignificant.

Differences in S. validus stem heights between transplant, control, and undisturbed plots were significant at only the freshwater site (Fig. 4-2). Transplants at the freshwater site had significantly smaller stem heights than undisturbed plots and were significantly smaller than the mean stem height at oligohaline and mesohaline sites. At both freshwater and mesohaline sites, control plots had significantly greater stem heights than S. validus transplanted from the oligohaline site.

Stem densities of transplants to freshwater and mesohaline sites decreased to densities that were not significantly different from those of the control plots at freshwater and mesohaline sites. Differences in stem densities between freshwater transplants that originated at the oligohaline site and control plots at the oligohaline site were significant. Differences between mesohaline transplants and oligohaline controls were not significant. Undisturbed plots of S. validus at the oligohaline site also had greater densities when compared with plots transplanted to freshwater and mesohaline sites.

Differences in mean stem densities of S. validus between transplant, control, and undisturbed plots were not significant at any of the 3 sites (Fig. 4-2).

Transplants to the freshwater site were invaded predominantly by Eleocharis montevidensis, Hydrocotyle umbellatum, and Aster spp. Zizaniopsis miliaceae and Typha latifolia, commonly co-occurring species with S. validus at the freshwater site, were rarely present in the transplants. Mesohaline transplants were invaded almost exclusively by Spartina alterniflora.

Light Extinction

Light extinction through the vegetation to the soil surface was significantly greater at the freshwater site when compared with the oligohaline and mesohaline sites (Fig. 4-3). Plant species and percent cover accounted for a significant amount of variation in light extinction within each marsh site (ANOVA; $F = 2.43$; $P = 0.01$; $n = 107$) (Table 4-1). Internode lengths were greatest, and stem heights and densities lowest for S. validus at sites where light penetration through the canopy was lowest.

Discussion

Detimental effects of increased salinities on plant growth were evident in decreased stem heights and densities of S. validus in greenhouse experiments. These results were similar to those for other studies in which salt tolerant species were found to grow best under freshwater or low

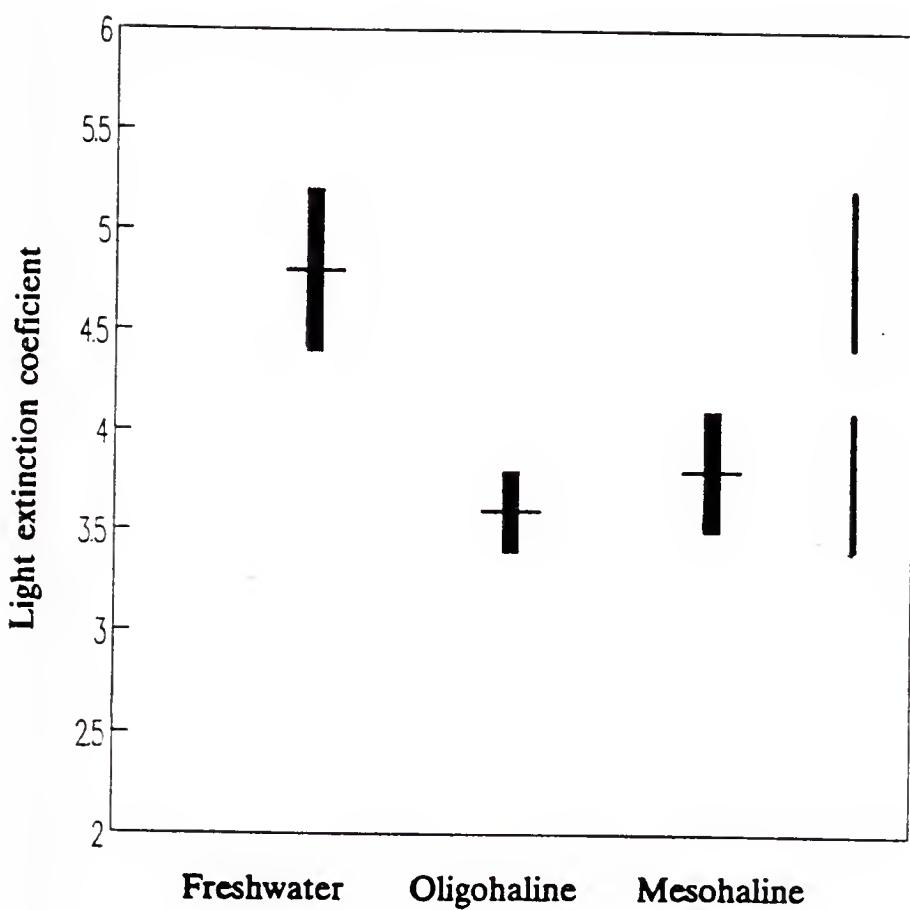


Fig. 4-3. Mean (± 1 SE) light extinction coefficients for freshwater, oligohaline, and mesohaline sites. Means falling within the same vertical line to the right of graph are not significantly different (Waller-Duncan, $P = 0.05$).

Table 4-1. Variation in light extinction coefficient between and within sites.

Source of variation	D.F.	F value
Marsh	2	5.76**
% Open canopy	10	2.79*
Species (marsh)	5	2.42**
Species (% open)	2	6.49**
Replicates (marsh)	18	1.42(N.S.)

*Significant at $P = 0.05$ level; **Significant at $P = 0.01$ level; N.S. = not significant.

salinity conditions (Phleger 1971, Jackson 1952, Parrondo 1978, Cooper 1982, Seneca 1969), indicating that higher salinities inhibit growth in these species.

Transplants of S. validus growing at the freshwater site exhibited a significant decrease in stem heights and densities compared with the mesohaline transplant site and oligohaline donor site. In both greenhouse and transplant experiments, however, variation in morphology was not related to the salinity of the area from which the plants were taken, suggesting that morphological variation in S. validus is not genetically fixed. Variation was dependent upon local conditions rather than plant origin, and demonstrates that changes in S. validus morphology across a salinity gradient are ecophenic, rather than ecotypic, responses.

Salinity has been found to have an overriding effect on growth and survival in some experiments with Salicornia europeae (Ungar 1987). In contrast, several studies have concluded that competition, disturbance, light penetration, and herbivory were more important in the growth and distribution of this particular species (Ellison 1987), as well as others (Bertness and Ellison 1987). While S. validus exhibited plastic responses to environmental conditions in both greenhouse and transplant experiments, growth patterns were reversed between the two. Greenhouse plants grew better at 0 ppt, while field transplants did

better at 5 and 10 ppt. Salinity had no effect on internode length in greenhouse treatments, but field measurements of internode lengths differed between freshwater, oligohaline, and mesohaline field sites.

Discrepancies in stem heights, stem densities, and internode lengths between greenhouse experiments and field transplants indicate morphological plasticity observed in S. validus. S. validus was not solely attributable to salinity. Factors other than salinity appeared to be important in the actual distribution and growth morphology of S. validus. Scirpus validus transplanted to the freshwater site was unable to expand into immediately adjacent areas, where other species were already present and overall stem densities were high. Internode lengths at field sites were greater, averaging 2.2 cm, compared with an average of 0.5 cm in greenhouse plants. Greenhouse plants, because they were planted at low densities without other species present, could expand into open areas where there was plenty of light and produce shorter internode lengths and closely arranged stems.

Transplants of S. validus were invaded at both freshwater and mesohaline sites by neighboring species until densities and species composition reached those of undisturbed plots at their respective transplant sites. These changes suggested that interspecific competition may be important in the morphology and distribution of S. validus. Decreases in stem heights and densities, and

invasion of S. validus transplants by salt intolerant species at the freshwater site may be due to greater competition from freshwater species under these conditions.

Physiological specialization on a widely distributed habitat type (e.g., freshwater marsh) results in ecological generalization, whereas physiological generalization to several habitat types (e.g., freshwater and brackish marshes) results in ecological specialization (McNaughton and Wolf 1970). Scirpus validus, a physiological generalist, may be outcompeted at the freshwater site by physiological specialists (e.g., Eleocharis montevidensis and Typha latifolia) because it cannot compete with the specialist within the specialist's range of physiological tolerance.

Salinities at the oligohaline site were high enough to inhibit freshwater species and low enough that stem heights and densities of S. validus were highest, internode lengths were shortest, and Spartina alterniflora was unable to expand into the site any farther than river and creek edges. Transplants at the mesohaline site exhibited decreased stem heights and densities, and were invaded by S. alterniflora. It may be that S. validus is not as great a physiological generalist as S. alterniflora. Spartina alterniflora, more tolerant of higher salinities, was able to invade and limit the growth of S. validus, probably due to inhibitory effects of higher salinities on S. validus.

Previous studies (Barbour 1978, Rabinowitz 1978) have noted that plant species' distributions often do not coincide with their physiological tolerances and that competitive interactions may be responsible for displacement of species from a habitat. Species' physiological tolerances and competitive interactions have also been shown to differ along an environmental gradient; physiological tolerance may limit a species at one end of an environmental gradient where conditions are relatively harsh, while competitive interactions may be of greater importance along the other, more benign portion of the gradient (Grace and Wetzel 1981, Snow and Vince 1984, Wilson and Keddy 1986).

Differences in morphology and densities for S. validus appear to be a result of differences in relative competitive abilities and salt tolerance between S. validus and other species. Scirpus validus was outcompeted at the freshwater site due to greater competitive abilities of other species, while it was limited by its own salt intolerance and decreased competitive ability at the mesohaline site. More specifically, differences in transplanted S. validus may be a result of light extinction differences between sites and the ability of S. validus to compete for available light by morphological adaptation to differential light regimes. Light-related morphological changes such as internode elongation may confer a competitive advantage on a species by enabling the plant to expand into less light-limiting

vegetation or gaps. Morphological variation and decreased survival have been associated with decreased light penetration in Salicornia europaea (Ellison 1987), and decreases in mean internode length have resulted from shading in submersed freshwater macrophytes (Spence and Dale 1978, Barko and Smart 1981, Barko et al. 1982). Numbers of species and subsequent differences in canopy layers and complexity accounted for a significant amount of the variation in light extinction within each marsh site. Differences in morphology at field sites may be a result of responses to light limitations placed on S. validus by neighboring individuals.

Morphological variation has been used to illustrate competitive interactions among animal species. Data on the morphology of birds (Van Valen 1965), lizards (Lister 1976a), and harvesting ants (Davidson 1978) provide evidence that variation in morphology increases as interspecific competition and the number of species decreases. This may further explain why morphological differences in S. validus coincide with species numbers more so than salinity gradients. Coefficients of variation for field measurements of S. validus stem heights and internode lengths were lowest at the freshwater marsh, where species numbers were greatest. While examples of morphological variation have most often been described for species in relatively harsh environments, for example, salt marshes, deserts, and

exposed mountain slopes, and may reflect steep environmental gradients in these habitats, results of this study demonstrate that morphological variation observed for S. validus is not directly due to a strong environmental gradient. A reduction in the range of morphological variation expressed by S. validus in the freshwater marsh may be due to increased species numbers and competitive interactions and may account for the lower variation in stem height and internode length in S. validus at this site. Conversely, decreased species numbers and fewer competitive interactions at higher salinities may allow a greater range of morphological expression at the mesohaline site.

In conclusion, different growth morphologies in S. validus are ecophenic responses to local abiotic and biotic conditions. While salinity alone is not responsible for variation in measured plant characteristics, it greatly affects species composition, which in turn may reflect the degree of physiological specialization and competitive ability of species in freshwater and low salinity marshes. Species composition also affects light availability. Not only is light an important resource for which plants compete, but it also influences morphological variation in several species, and light appears important in S. validus as well. Morphological variation in S. validus further indicates differences in the degree of competitive

interactions between plants of tidal freshwater and brackish marshes along the lower Savannah River.

CHAPTER 5

THE ROLE OF COMPETITIVE INTERACTIONS, SOIL SALINITY, AND DISTURBANCE IN THE DISTRIBUTION OF TIDAL MARSH PLANT SPECIES

Introduction

Plant species of tidal freshwater marshes are numerous and have narrow, well differentiated niches (Odum 1988), in comparison with saline marshes, suggesting that competitive hierarchies are well developed and competition among species is diffuse rather than species-specific. Freshwater species distributions may reflect better developed and more complex competitive interactions characteristic of late successional, environmentally benign communities. In contrast, brackish marsh vegetation is more strongly influenced by salinity-induced physiological stress and steeper environmental gradients (Phleger 1971, Kruczynski et al. 1978) characteristic of relatively early successional communities. Species in such harsh environments generally have broadly overlapping resource requirements, resulting in more intense competitive interactions (Parrish and Bazzaz 1982), as well as altered dominance hierarchies (Anderson 1986).

Few experiments have directly addressed the role of competitive interactions in species distributions along environmental gradients (see Chapter 4). Pair-wise species

competition experiments across a gradient of stress and disturbance have demonstrated lower competitive abilities for species where environmental stress is greater. Conversely, where conditions are more benign, competitive abilities are greater (Wilson and Keddy 1986). The combined consequences of competition and environmental gradients on plant interactions have not been directly examined. Studies of salt marsh species distributions have shown that, in addition to physical factors, species interactions (Bertness and Ellison 1987, Bertness and Ellison 1987, Snow and Vince 1984) are important to plant community structure. Several of these studies have also implied that along an environmental gradient, competitive interactions may determine species distributions at one end of the gradient, while physiological tolerance may limit species distributions at the other.

In addition to the effects of physical factors and species interactions, plant species abundance and composition in mixed species salt marshes can be altered (Bakker 1985), plant regeneration inhibited (Chabreck 1968), and net aboveground primary production reduced (Turner 1987) as a result of trampling by foraging animals. Soil disturbance from rooting and trampling by feral hogs often results in a reduction of herbaceous cover and local extinction of some plant species (Bratton 1974). These changes have not, however, been documented in freshwater

tidal marshes. A large feral hog population inhabits freshwater and oligohaline regions of the study area and may significantly affect plant community structure. Vegetation response to such disturbances will help define the role of disturbance in structuring freshwater tidal marshes.

The objective of this study was to examine the role of competition in structuring plant communities across a salinity gradient of freshwater, oligohaline, and mesohaline tidal marshes and to document possible effects of animal disturbance. Species interactions occur at the level of individual neighbors (Mack and Harper 1977, Fowler and Antonovics 1981) and the distribution of a single species may affect larger scale community structure (Mack and Harper 1977, Fowler and Antonovics 1981, Dale 1986). Because of this, I chose to use *Scirpus validus*, the only species which occurred throughout the salinity gradient, as the primary indicator species in examining the distribution of species as a function of competitive variation along this gradient.

Two general hypotheses were proposed: (1) *S. validus*, the species with the widest range of occurrence, was restricted under freshwater conditions by more specialized species better able to compete for resources, (2) at higher salinities, physiological tolerance is more important in limiting the distribution of *S. validus*. Removal and addition of species in both field and greenhouse experiments, combined with reciprocal transplants of species

across the salinity gradient, were used to test these hypotheses. Competitive ability was measured as relative increases in biomass and density. A third hypothesis proposes that disturbances created by feral hog activities will result in a local reduction in species diversity. Disturbance was measured as the change in abundance of species following feral hog activities.

Differences in competitive ability along an environmental gradient should be apparent for a species such as S. validus because of its wide distribution. The range of salinity tolerance exhibited by S. validus indicated that it is a physiological generalist, and should therefore be competitively unsuccessful in combination with physiological specialists within the range of the specialist(s). In the freshwater marsh, removal of neighbors would be expected to enhance the growth and expansion of S. validus, while removal of S. validus may or may not have a significant effect on neighboring freshwater species. Transplants of S. validus into freshwater marsh from monospecific stands in oligohaline marsh should succumb to the greater competitive abilities of freshwater species.

Increased salinities of oligohaline and mesohaline marshes place greater physiological stress on plant species and zonation of species was conspicuous. Scirpus validus may have occurred in high marsh zones because of its competitive superiority over other marsh species at the less

stressful higher elevations, and be restricted from the low marsh by a physiological intolerance of frequent flooding. Competition under these conditions was expected to favor the species with the broader salinity tolerance, e.g. S. alterniflora, and result in greater competitive interactions between S. validus and other species.

Methods

The study sites included freshwater (<1 ppt), mildly oligohaline (2-4 ppt), strongly oligohaline (5-7 ppt), and mesohaline (8-10 ppt) tidal marshes of the lower Savannah River, in Chatham County, Georgia, and Jasper County, South Carolina (see Chapter 2). The high energy, dynamic conditions of tidal marshes maintain these systems in an early successional stage (de la Cruz, A.A. 1981), while the salinity gradient from freshwater to brackish marshes creates a natural stress gradient. Tidal marshes of the lower Savannah River provided an opportunity to examine competitive interactions among plant species across a salinity gradient.

Eleocharis montevidensis was a dominant species co-occurring with S. validus in the freshwater marsh along with several freshwater annuals. Spartina alterniflora is the co-dominant species under mesohaline conditions. At mildly oligohaline conditions, the dominant species are Zizaniopsis miliacea and S. validus. Strongly oligohaline conditions support very few species other than S. validus.

All statistical analyses were carried out using SAS (Statistical Analysis System, Cary, North Carolina, 1988).

Field Transplants Between Sites

To determine the response of vegetation to changing soil salinities and species associations, between-site transplants of dominant species from freshwater, oligohaline, and mesohaline marshes were made between marshes. In December 1987, transplant, control, and undisturbed plots were established at freshwater, mildly and strongly oligohaline, and mesohaline sites to be transplanted between sites. Eighteen previously established, undisturbed plots at each site were used for comparison with controls. A Reichert refractometer was used to measure and monitor soil water salinities at field sites. At random points, plant contents of 0.25 m X 0.25 m plots, approximately 15 cm deep, were collected from donor sites and transplanted to random points at recipient marsh sites. The same size control plots were removed and then replaced at each donor site to determine if transplanting effects were significant. Rubber lawn edging (10 cm deep) was placed around all between site transplants to inhibit belowground competition. PVC flags were placed 0.25 m deep into the marsh at corners of transplants to delineate plots.

Twenty S. validus plots were transplanted from the donor oligohaline site to the freshwater site, and 20 to the mesohaline site. Twenty control plots were established.

Twenty plots from the donor freshwater marsh were transplanted to the strongly oligohaline site, and 10 to the mesohaline site. Twenty five control plots were established at the freshwater donor site. Twenty plots were transplanted from the mesohaline donor site to the oligohaline site, and 10 to the freshwater site. Twenty five control plots were established at the mesohaline site.

Above-ground vegetation from transplants and controls was harvested in June, 1989. Undisturbed plots were harvested in June, 1988. Plants were identified, counted, dried, and weighed.

Analysis of variance was used to determine if differences among donor plots transplanted to different marsh sites were significant. LSD tests, which are pairwise t-tests equivalent to Fisher's least-significant difference test for unequal sample sizes, were used to compare biomass and density for donor marsh plots transplanted to freshwater, oligohaline, and mesohaline sites.

Field Transplants Within Sites

To examine differences in competitive ability among species within a site, within-site transplant comparisons were made between inner and outer plots and their control plots. Changes in within-site transplants were also compared between marsh sites to determine whether differences in competitive interactions varied along the salinity gradient.

At freshwater, mildly oligohaline, and mesohaline marsh sites, 75 sets of transplants, at 25 randomly chosen points at each site, were established in December, 1987. Each set of transplants consisted of a S. validus control plot, a neighbor control plot, and a S. validus experimental plot nested into the larger neighbor plot.

Control and experimental S. validus plots were 0.25 m long X 0.25 m wide X 0.15 m deep. Neighbor plots were 1.0 m long X 1.0 m wide X 0.15 m deep, with a section removed from the center; experimental S. validus plots were nested in the center of neighbor plots. Control plots were removed and replaced for both S. validus and neighbor plots. Rubber garden edging was placed 0.10 m deep around 1.0 m X 1.0 m neighbor plots to inhibit interactions between experimental plots and surrounding vegetation. PVC flags were placed 0.25 m deep into the marsh at corners of all plots so that vegetation could be harvested separately for controls, neighbor, and experimental S. validus plots.

All species except S. validus were clipped and removed from inner S. validus plots and all S. validus was removed from outer neighbor plots in April, 1988. Clipping and removal of species was repeated in June and August, 1988. Above-ground vegetation was harvested from all plots in June, 1989. Vegetation was sorted by species, and stems were counted and dried to a constant weight. Relative proportions by weight and density were calculated for S.

S. validus, S. alterniflora, Z. miliaceae, and E. montevidensis and an "other" category for transplants at each site.

Differences between outer neighbor controls and inner S. validus plots enabled a determination of relative increase, decrease, or no change with the removal of neighbor species. Control S. validus plots were compared with inner S. validus plots to determine changes in S., especially for mildly oligohaline and mesohaline sites where control S. validus plots rarely contained any other species. Differences between neighbor controls and outer neighbor plots were used to determine effects of the removal of S. validus on neighbor species. Differences between inner S. validus and outer neighbor plots at each marsh site were calculated and compared to determine the overall effects of the combined removal of neighbor species from inner plots and S. validus from outer plots.

Paired t-tests were used to determine if differences among controls, neighbor plots, and experimental S. validus plots were significant. Pairwise t-tests were used to compare differences between freshwater, mildly oligohaline, and mesohaline sites ($P < .05$).

Greenhouse Experiments

To examine the potential for competition between S. validus and freshwater species at varying salinities, a series of DeWitt experiments (Silvertown 1982) were set up in a greenhouse at the Center for Wetlands, Univ. of

Florida, in December, 1988. Randomly chosen plots of freshwater marsh were collected in 0.25 cm diam. x 0.20 cm deep pots. Ramets of S. validus were also randomly collected. Fifteen pots contained no S. validus, 15 contained 10% S. validus, 15 contained 30% S. validus, 15 contained 50% S. validus, and 15 contained 100% S. validus. Five pots from each group were placed in each of 3 treatment pools, and watered daily with 0, 5, and 10 ppt seawater solution, respectively, for 6 months. Soil water salinities were monitored using a Reichert refractometer. The five pots containing freshwater species but no S. validus were also used to determine the effects of increasing salinity on freshwater marsh species.

Above-ground vegetation was harvested from all plots in July, 1989. Vegetation was sorted by species and stems were counted and weighed. Total and individual relative yield by weight and density were calculated for S. validus and the combination of other species for each pot.

Two-way analysis of variance was used to test for significant effects of salinity and initial proportions of S. validus on relative and total yields of S. validus and the combined other species. The T-method for multiple comparisons among nearly equal sample sizes (Sokal and Rohlf 1981) was used to compare differences in effects of initial S. validus proportions between freshwater, oligohaline, and mesohaline treatments.

Feral Hog Disturbance

A 0.5 km² study area was established in an area dominated by giant cutgrass, softstem bulrush, cattail (*Typha angustifolia*), and spikerush (*Eleocharis montevidensis*). Cypress, tupelo, and sweetgum (*Liquidambar styraciflua*) grew along adjacent river levees. Interstitial soil salinities averaged 4 ppt.

Thirty 1.0 m² sample plots initially intended for plant competition experiments were established in the study area in December 1987. Vegetation sampling plots were located in stands with an even mix of *Z. miliaceae* and *S. validus* (50% cutgrass, 50% bulrush) at 6 random points along each of 5 transects in the study area.

Six of 12 study plots showed signs of trampling or rooting by feral hogs in January 1988. Percent cover of cutgrass and species composition of remaining vegetation was measured in disturbed and undisturbed plots during March and April 1988. Student's T-test was used to compare percent cover of disturbed and undisturbed plots.

Results

Control plots did not differ significantly from undisturbed plots at any transplant sites, indicating that transplanting within sites had no effect on vegetation. Subsequently, only comparisons between controls and experimental plots are presented.

Between-site Transplants

Changes in proportions of dominant species for plots transplanted to different sites are given in Figure 5-1.

Relative density and biomass of E. montevidensis decreased significantly after being transplanted to the mesohaline site, but remained unchanged relative to the control when transplanted to the oligohaline site ($P = 0.05$). Relative density of S. validus transplants at the mesohaline marsh decreased significantly ($P = 0.05$), while relative biomass decreased significantly at both freshwater and mesohaline sites. Spartina alterniflora decreased significantly ($P = 0.05$) in relative density and biomass when transplanted to the freshwater site, but not the oligohaline site.

Donor transplants at the freshwater marsh site were invaded by local species and showed no difference in species composition, biomass, or density when compared with freshwater marsh controls (Fig. 5-2). Donor transplants from the oligohaline marsh, composed predominantly of S. validus, decreased significantly in S. validus biomass ($F = 6.43$; $DF = 2$; $P < .05$) and density ($F = 38.44$; $DF = 2$; $P < .05$) after transplanting to the freshwater marsh site.

Spartina alterniflora from the mesohaline marsh decreased significantly in biomass ($F = 9.26$; $DF = 2$; $P < .05$) and density ($F = 3.45$; $DF = 2$; $P < .05$). Eight of the 10 initial transplants of S. alterniflora from the mesohaline marsh were still intact when harvested; two were lost to

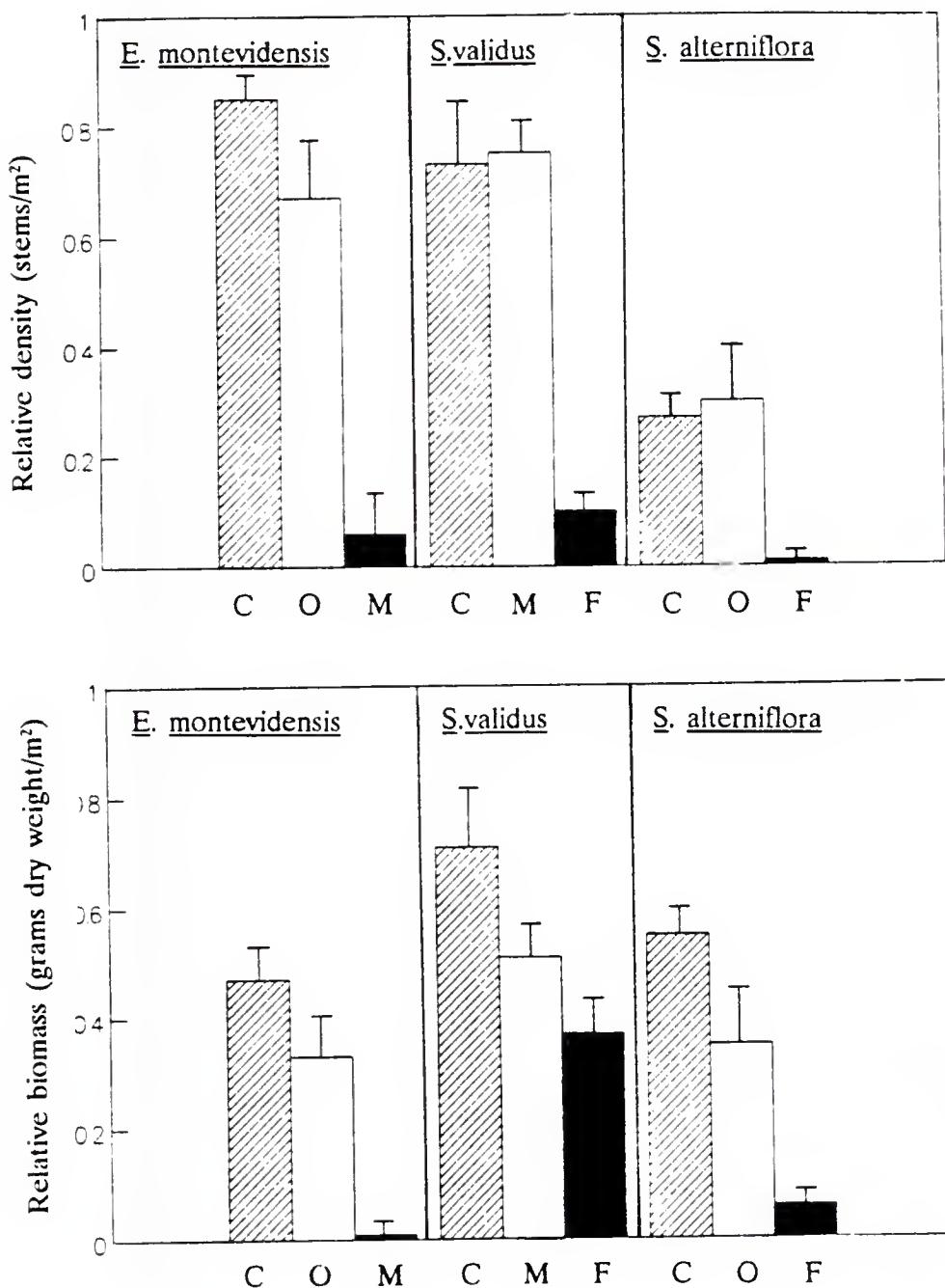


Fig. 5-1. Means and standard errors for relative densities and biomass of: *E. montevidensis* transplanted from freshwater marsh to oligohaline and mesohaline marsh; *S. validus* transplanted from oligohaline to mesohaline and freshwater marsh; and *S. alterniflora* transplanted from mesohaline to oligohaline and freshwater marsh (see methods section for details). C = control, F = freshwater, O = oligohaline, M = mesohaline site.

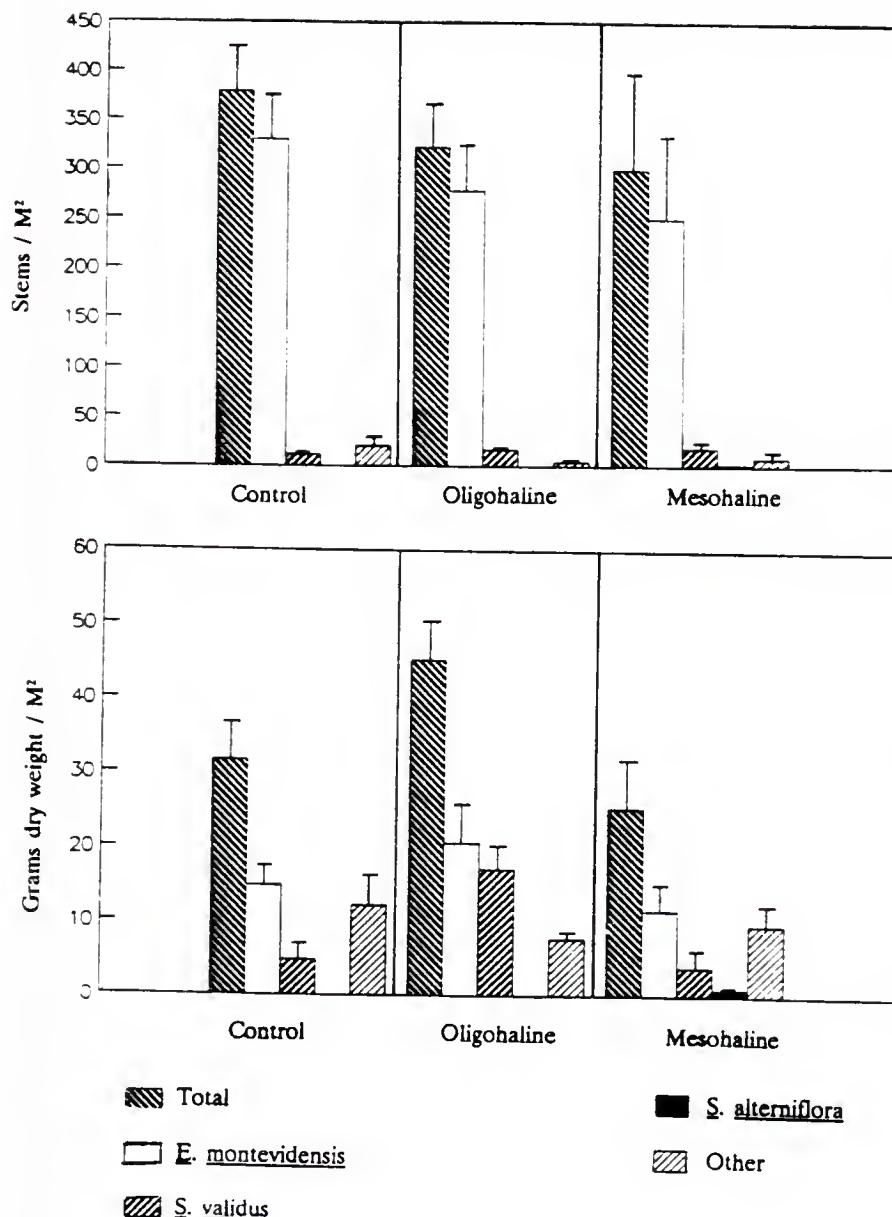


Fig. 5-2. Total and individual means and standard errors for species density and biomass for oligohaline and mesohaline donor transplants and controls at freshwater site.

feral hog disturbance. Three of the 8 plots had 2-4 small S. alterniflora remaining.

Plant biomass was significantly less in donor plots transplanted to the oligohaline site ($F = 54.18$; $DF = 2$; $P < .05$) when compared with the oligohaline controls (Fig. 5-3). Unlike plots transplanted to the freshwater marsh, donor transplants at the oligohaline marsh were not as readily replaced by local vegetation. Scirpus validus and the "other" category made up the biomass in the control plots; the "other" category contained almost exclusively Typha angustifolia and Zizaniopsis miliacea. Neither E. montevidensis from the freshwater marsh nor S. alterniflora from the mesohaline marsh decreased in biomass or density after being transplanted to the oligohaline marsh when compared with their respective controls. Plant densities were greatest for donor freshwater marsh plots ($F = 12.08$; $DF = 2$; $P < .05$), where E. montevidensis reached densities twice that of total densities in the oligohaline control plots, although it was restricted to donor freshwater transplants. In addition to its survival in donor mesohaline transplants, S. alterniflora invaded donor freshwater transplants. Oligohaline control plots were not invaded by S. alterniflora. The oligohaline site was the only site at which edging around plots appeared to inhibit invasion by neighbor species.

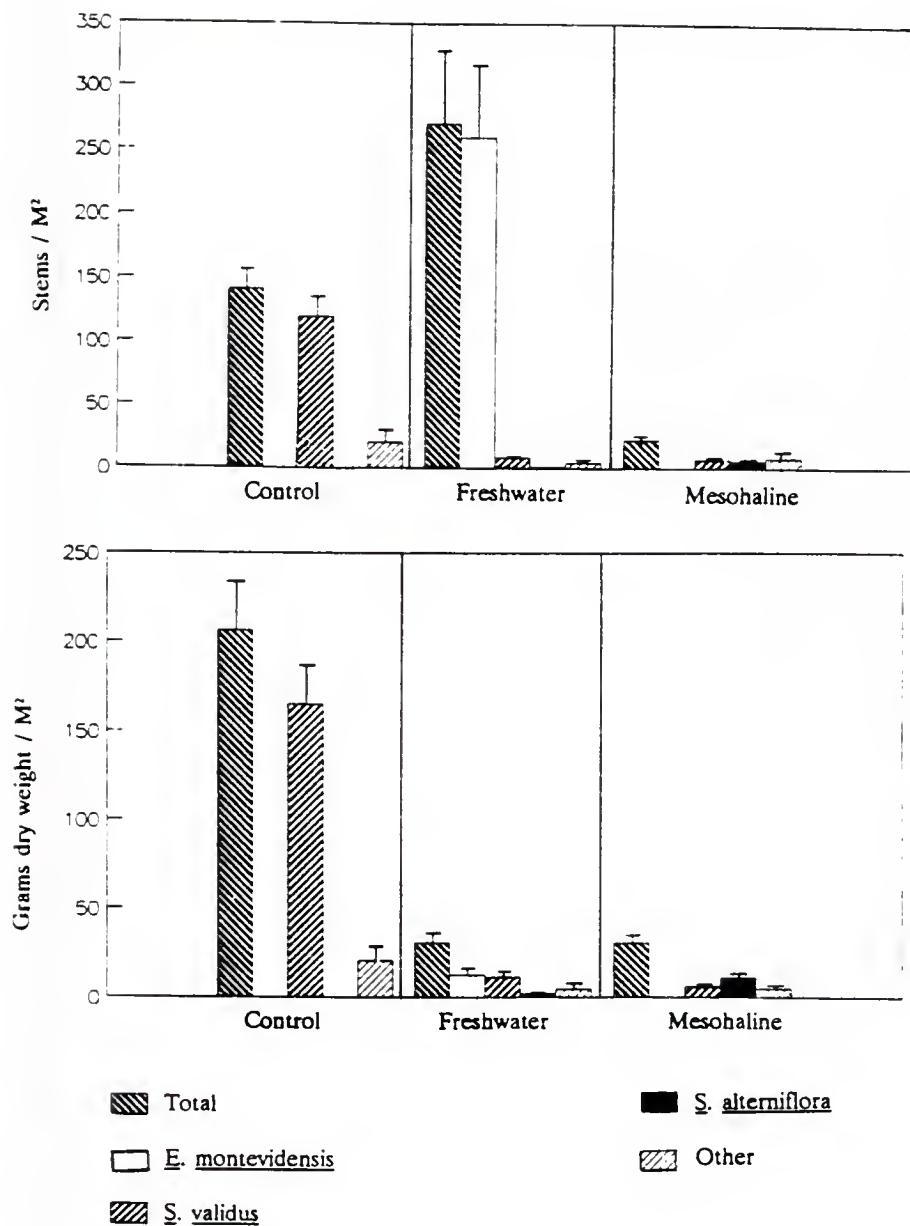


Fig. 5-3. Total and individual means and standard errors for species density and biomass for freshwater and mesohaline donor transplants and controls at oligohaline site.

All donor plots at the mesohaline marsh were invaded successfully by S. alterniflora as well as small amounts of Scirpus robustus. Donor transplants at the mesohaline marsh did not differ in density or biomass of invading S. alterniflora at the end of the experiment, although total density ($F = 4.94$; $df = 2$; $P < .05$) and biomass ($F = 3.20$; $DF = 2$; $P < .05$) were significantly less in freshwater donor transplants (Fig. 5-4). Donor transplants did not differ in the biomass or density of S. validus remaining when compared to mesohaline control plots. Donor freshwater transplants had significantly less biomass and density compared with oligohaline donor plots and mesohaline controls, a result of less S. validus in these transplants. Variance associated with these plots was high, however, due to the relatively small number of transplants (10), and differences in S. validus between these and other plots were not significant. The initially dominant species in freshwater donor transplants, E. montevidensis, significantly declined when transplanted from freshwater to mesohaline marsh in both biomass ($F = 11.93$; $DF = 2$) and density ($F = 23.67$; $DF = 2$); only one donor freshwater plot had E. montevidensis remaining.

Within-site Transplants

Inner S. validus vs. outer control plots. A comparison of inner S. validus plots and outer controls was made to determine if S. validus had increased beyond the abundance

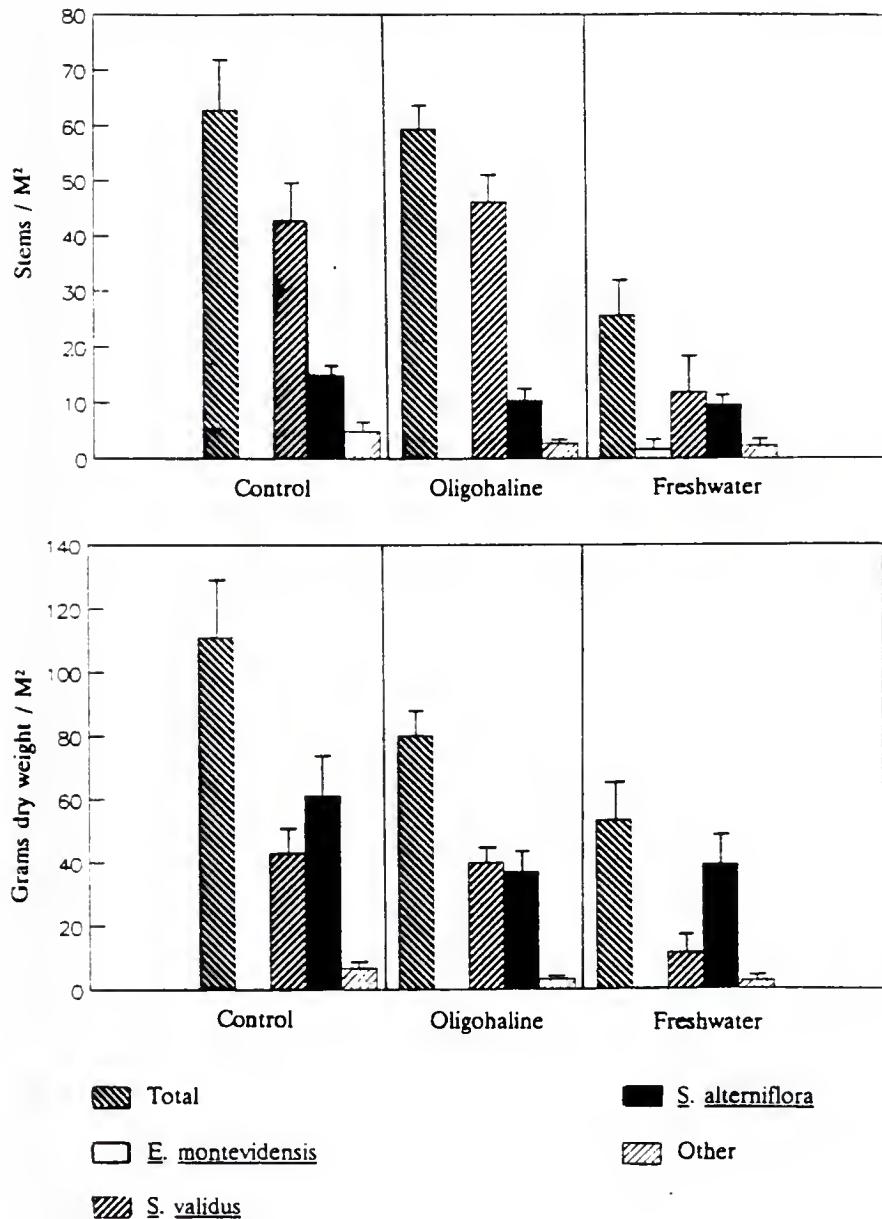


Fig. 5-4. Total and individual means and standard errors for species density and biomass for freshwater and oligohaline donor transplants and controls at mesohaline site.

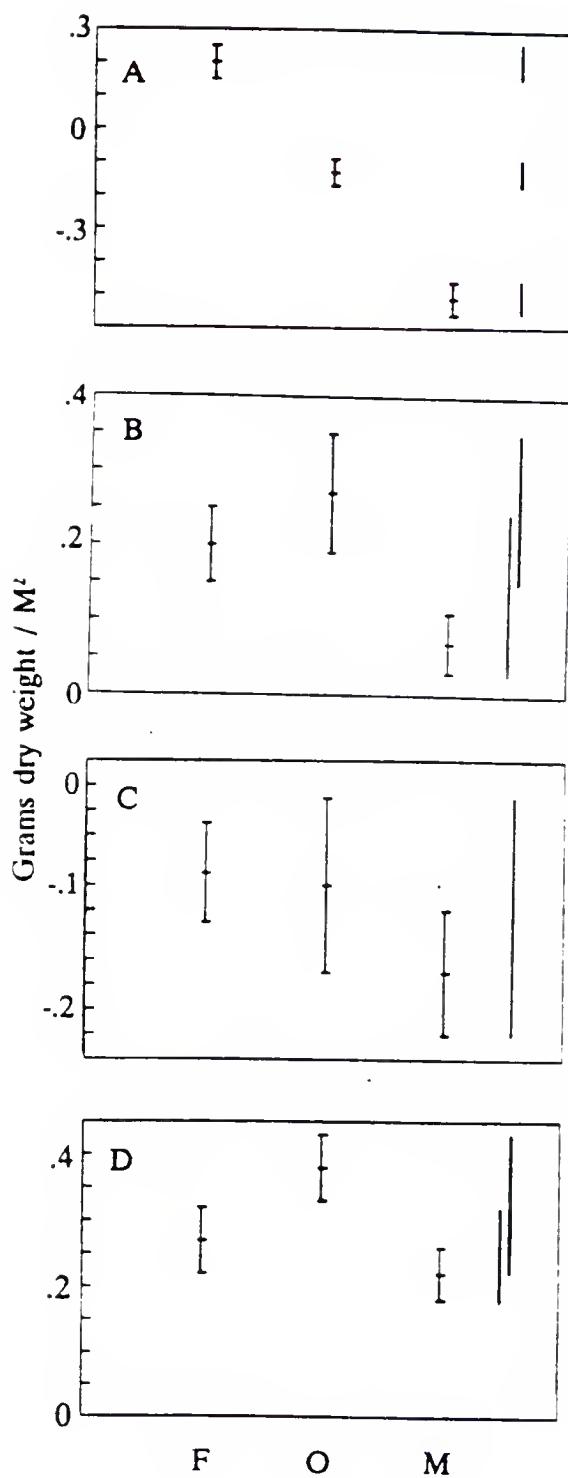
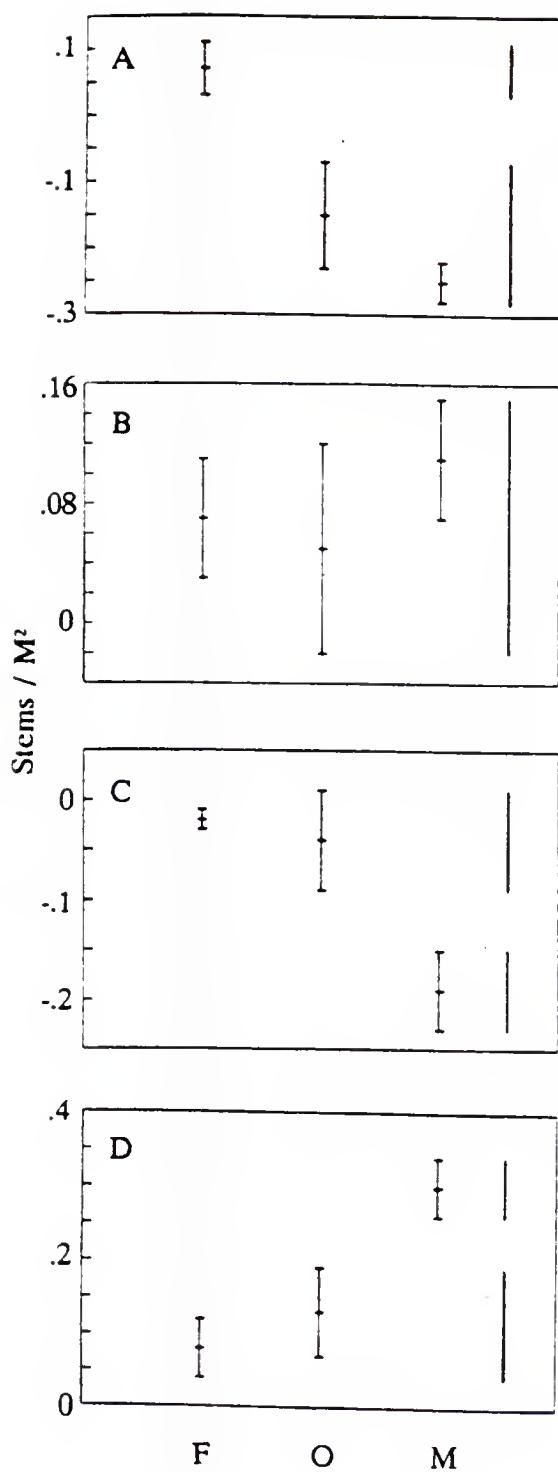
expected in mixed plots (rather than monospecific S. validus plots). Clipping and removal of neighbor species from inner plots resulted in increases in S. validus biomass at freshwater and oligohaline sites, but not mesohaline (Fig. 5-5). While densities of initially monospecific S. validus plots remained greater than for neighbor control plots only at the mesohaline site ($t = 3.10$; $N = 25$; $P < .005$), the difference in density between inner plots and neighbor controls at the mesohaline site was no greater than differences at freshwater and oligohaline sites.

Biomass of inner S. validus plots decreased to that of the neighbor control plots at the mesohaline site. Biomass of S. validus was greater at the oligohaline ($t = 3.41$; $N = 24$; $P < .01$) and freshwater sites ($t = 4.26$; $N = 26$; $P < .001$) when compared with neighbor control plots, but did not differ between these two sites. Differences in S. validus density between inner plots and neighbor controls were not significant for freshwater or oligohaline transplants.

Inner *S. validus* vs. control *S. validus* plots.

Initially monospecific inner plots of S. validus exhibited the greatest decrease in S. validus at the mesohaline site, while similarly monospecific plots at the mildly oligohaline site showed relatively little, if any, change (Fig. 5-5). The effects of clipping and removal of neighbors were not apparent in a comparison of mildly oligohaline and mesohaline transplants relative to control S. validus plots

Fig. 5-5. Means and standard errors for differences in relative density and biomass between (A) inner S. validus and inner control plots, (B) inner S. validus (with neighbor species removed) and neighbor control plots, (C) outer neighbor (with S. validus removed) and outer control plots, and (D) inner S. validus and outer neighbor plots for freshwater, oligohaline and mesohaline sites. Separate solid lines at right of graph indicate significant differences between sites.



(although effects of removal can be seen when inner plots are compared with neighbor controls for these 2 sites in Fig. 5-5).

Effects on S. validus biomass following transplanting into neighbor plots were significant at all 3 sites (Fig. 5-5). Scirpus validus biomass in inner plots increased at the freshwater site ($t = 4.21$; $df = 26$; $P < 0.01$), but decreased at oligohaline ($t = -3.06$; $df = 24$; $P < 0.01$) and mesohaline ($t = -10.01$; $df = 25$; $P < 0.01$) sites, where inner S. validus transplants at both sites initially contained only S. validus. Changes in S. validus biomass were of a significantly smaller magnitude at the oligohaline site when compared with freshwater and mesohaline sites ($F = 55.38$; $df = 2$; $P < 0.05$). Differences in density between inner S. validus and control plots were significant only at the mesohaline site ($t = -7.94$; $df = 25$; $P < 0.05$). Differences in Scirpus validus density between inner S. validus and control S. validus plots were not significant between oligohaline and mesohaline sites, although freshwater plots had significantly greater densities when compared with oligohaline and mesohaline plots ($F = 9.32$; $df = 2$; $P < 0.05$).

Inner S. validus at the freshwater site were the only plots to show an increase in S. validus, due to the fact that, unlike control plots at other sites, freshwater inner control plots were not almost exclusively S. validus (Fig.

5-5). Inner plots at the freshwater site were not completely filled by S. validus in the space made available by removal of other species, although inner plot densities were approximately 10% greater and biomass 20% greater for S. validus control plots. The species most common in the inner freshwater plots at harvest was E. montevidensis.

Inner S. validus plots at the oligohaline site decreased significantly in density, but still had near-zero differences when compared to control plots of pure S. validus, and there were no differences in biomass between inner and control plots of S. validus (Fig. 5-5). Some invasion of inner plots by species other than S. validus occurred at the oligohaline site, predominantly by E. montevidensis.

Decreases in density and biomass of S. validus were greatest at the mesohaline site (Fig. 5-5). Mesohaline plots had significant net losses for both density and biomass of S. validus, and changes were of a significantly greater magnitude than for freshwater or oligohaline transplants. Removal of neighbor species at the mesohaline site resulted in the invasion of available space by species other than S. validus, predominantly S. alterniflora.

Outer neighbor vs. neighbor control plots. Only the mesohaline site exhibited a significant change in S. validus biomass in the outer neighbor plots when compared with control plots ($t = -3.19$; $df = 25$; $P < .01$) (Fig. 5-5),

resulting in less S. validus (and more S. alterniflora) in outer neighbor plots. The removal of S. validus from neighbor plots also resulted in a significant decrease in S. validus densities at only the mesohaline site at the end of the experiment.

Removal of S. validus did not result in decreases in S. validus biomass relative to control plots at the freshwater site (Fig. 5-5). Scirpus validus maintained densities similar to control plots for oligohaline transplants as well, which were initially monospecific S. validus. The difference in S. validus biomass between outer neighbor and neighbor control plots did not vary different among sites.

Removal of S. validus from outer neighbor plots had no significant effect on S. validus densities at the oligohaline site and S. validus in outer neighbor plots recovered and reached densities similar to controls (Fig. 5-5). Decreases in S. validus densities in the outer neighbor plots were significantly less at freshwater and oligohaline sites when compared with the mesohaline site ($F = 6.52$; $df = 2$; $P < .05$).

Inner S. validus vs. outer neighbor plots. Combined removal of S. validus from outer neighbor plots and removal of neighbor species from inner plots resulted in significant differences in S. validus biomass and densities at all sites (Fig. 5-5). These results were due primarily to a net gain of S. validus in inner plots, combined with relatively no

loss of S. validus in outer neighbor plots at freshwater and oligohaline sites (Fig. 5-5). Mesohaline differences, on the other hand, reflected a decrease in S. validus from inner plots and an increase in S. alterniflora in outer neighbor plots.

Inner S. validus plots had significantly greater ($P < .01$) S. validus biomass than outer neighbor plots (from which S. validus had been removed during the previous spring and summer) at freshwater ($t = 5.86$; $df = 26$), oligohaline ($t = 7.41$; $df = 24$), and mesohaline ($t = 5.40$; $df = 25$) sites. Increases in S. validus densities were significant at oligohaline ($t = 2.13$; $df = 24$; $P < .05$) and mesohaline ($t = 7.50$; $df = 25$; $P < .01$) sites. Increases in S. validus biomass in inner plots relative to outer neighbor plots differed significantly between oligohaline and mesohaline sites ($F = 3.31$; $df = 2$; $P < .05$). The magnitude of differences in S. validus biomass between inner and outer plots did not differ significantly between oligohaline and freshwater sites or between mesohaline and freshwater sites. Relative increases in densities of S. validus were significantly greater ($P < .01$) at oligohaline ($t = 2.13$; $df = 24$) and mesohaline ($t = 7.50$; $df = 25$) sites. While S. validus biomass increased in inner plots at the freshwater site, S. validus densities did not change significantly.

Increases in S. validus densities in inner plots relative to outer plots were greatest at the mesohaline

site, where there was 30% more S. validus in the inner plot. Inner S. validus plots at freshwater and oligohaline sites had S. validus densities from 8 - 13% higher than outer plots, significantly less than plots at the mesohaline site ($F = 5.97$; $df = 2$; $P < .05$). Scirpus validus was replaced by predominantly E. montevidensis at freshwater and oligohaline sites, and by S. alterniflora at the mesohaline site.

Greenhouse Experiments

Plots containing only Scirpus validus

Relative yield of S. validus biomass and density in experimental plots was significantly affected by salinity treatment and initial proportion of S. validus (Table 5-1). Interaction effects between salinity and initial S. validus proportion were not significant in determining relative yields of S. validus density or biomass. Relative yields of S. validus densities were significantly greater at the mesohaline treatment when compared with the freshwater treatment, but did not differ between oligohaline and freshwater treatments or between oligohaline and mesohaline treatments ($MSE = 0.09$; $DF = 63$; $P = 0.05$). Density of S. validus was significantly greater at the mesohaline treatment when compared with oligohaline and freshwater treatments, but not between freshwater and oligohaline treatments ($MSE = 0.18$; $DF = 63$; $P = 0.05$). Biomass and

Table 5-1. Two-way ANOVA results of relative yield for A) biomass and B) density of S. validus in greenhouse experiments for the effects of salinity treatment (0, 5, 10 ppt) and initial proportion of S. validus (0, 10, 30, 50, 100 percent).

A.

Source of variation	df	MS	F
Salinity	2	0.43	4.66**
prop. <u>S. validus</u>	1	8.20	88.69**
Salinity X prop. <u>S. validus</u>	2	0.03	0.28 NS

**P < 0.001, *P < 0.01, NS = not significant.

B.

Source of variation	df	MS	F
Salinity	2	2.42	13.25**
prop. <u>S. validus</u>	1	9.05	49.54**
Salinity X prop. <u>S. validus</u>	2	0.00	0.99 NS

**P < 0.001, *P < 0.01, NS = not significant.

density of S. validus increased with increasing initial proportions of S. validus at all salinities (Fig. 5-6).

Plots containing all species except *Scirpus validus*

Initial proportions of S. validus had a significant effect on relative yield of biomass and density for all species combined (excluding S. validus), although salinity treatment did not (Table 5-2). Biomass and density of all species excluding S. validus decreased with increasing initial proportions of S. validus (Fig. 5-7). Interaction effects between salinity treatment and initial S. validus proportions were not significant in determining relative yields of total species excluding S. validus. Three species, E. montevidensis, Leersia virginica, and Scirpus robustus, were consistently present in pots at the mesohaline treatment at the end of the experiment. Other than S. validus, these 3 accounted for nearly all the biomass and density at the mesohaline treatment.

Plots containing all species

Salinity treatment and initial proportions had significant effects on total relative yield of biomass and density for all species in experimental plots (Table 5-3). Total relative yield of biomass and density were greater for mesohaline treatments when compared with freshwater and oligohaline treatments, while freshwater and oligohaline treatments showed no differences (MSE = 0.09; DF = 63; P = 0.05). Biomass and density of all species excluding S.

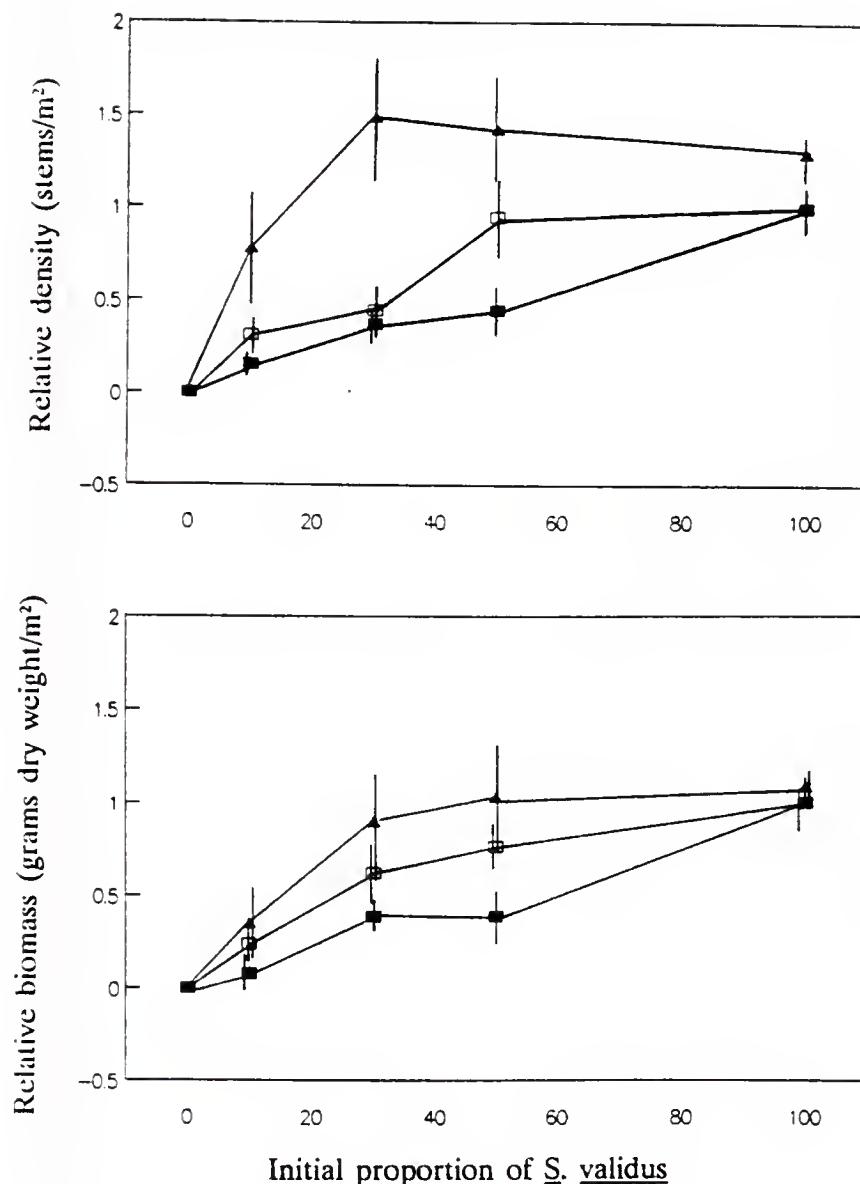


Fig. 5-6. Means and standard errors of relative yields for density and biomass of *S. validus* for different greenhouse soil salinities, plotted against initial *S. validus* density. Solid squares represent freshwater, empty squares represent oligohaline, and solid triangles represent mesohaline soil salinities.

Table 5-2. Two-way ANOVA results of relative yield for A) biomass, and B) density, of all species, excluding S. validus, in greenhouse experiments for the effects of salinity treatment (0, 5, 10 ppt) and initial proportion of S. validus (0, 10, 30, 50, 100 percent).

A.

Source of variation	df	MS	F
Salinity	2	0.01	0.28
prop. <u>S. validus</u>	1	0.33	76.93**
Salinity X prop. <u>S. validus</u>	2	0.00	0.69

**P < 0.001, *P < 0.01, NS = not significant.

B.

Source of variation	df	MS	F
Salinity	2	0.00	0.28
prop. <u>S. validus</u>	1	0.43	38.92**
Salinity X prop. <u>S. validus</u>	2	0.00	0.17 NS

**P < 0.001, *P < 0.01, NS = not significant.

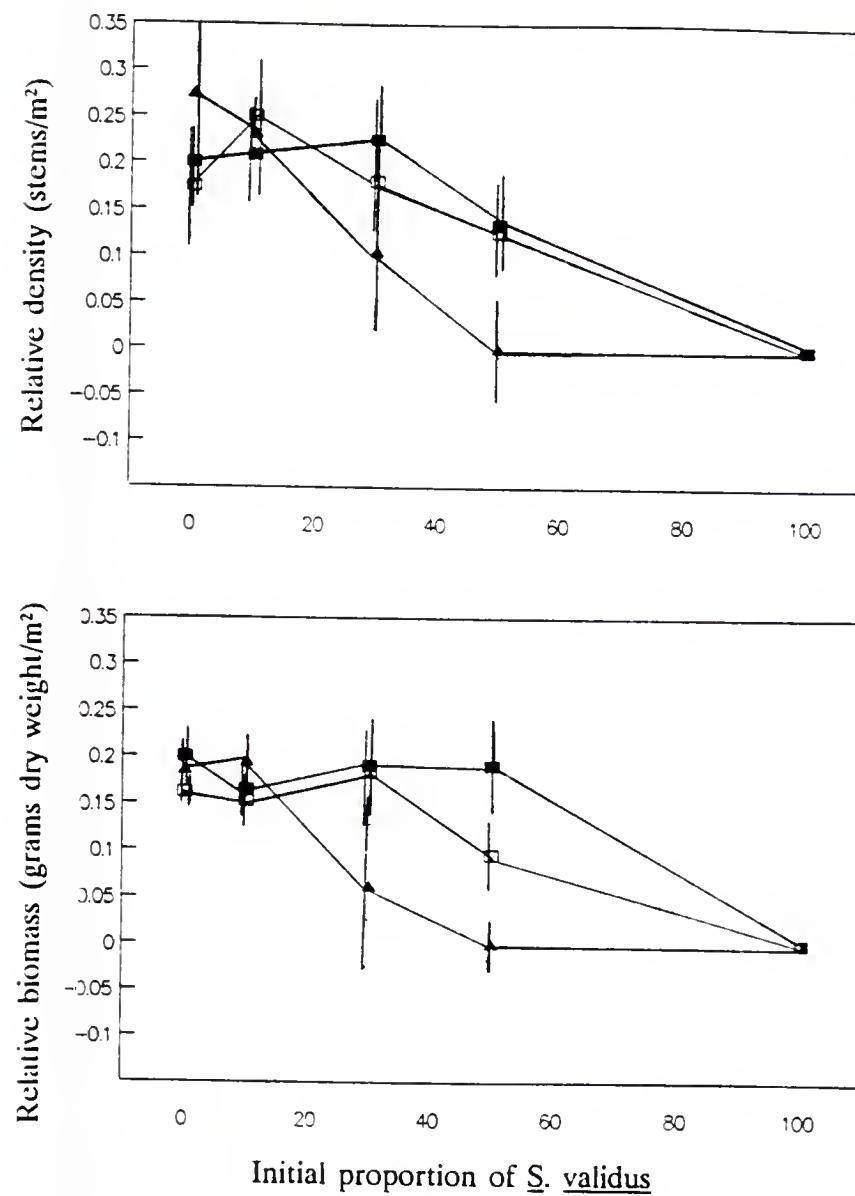


Fig. 5-7. Means and standard errors of relative yields for density and biomass of all species excluding *S. validus* for different greenhouse soil salinities, plotted against initial density of these species. Solid squares represent freshwater, empty squares represent oligohaline, and solid triangles represent mesohaline soil salinities.

Table 5-3. Two-way ANOVA results of relative yield for A) total biomass, and B) total density, of all species in greenhouse experiments for the effects of salinity treatment (0, 5, 10 ppt) and initial proportion of S. validus (0, 10, 30, 50, 100 percent).

A.

Source of variation	df	MS	F
Salinity	2	0.40	4.55*
prop. <u>S. validus</u>	1	5.23	58.77**
Salinity X prop. <u>S. validus</u>	2	0.04	0.45 NS

**P < 0.001, *P < 0.01, NS = not significant.

B.

Source of variation	df	MS	F
Salinity	2	2.59	12.97**
prop. <u>S. validus</u>	1	5.53	27.69**
Salinity X prop. <u>S. validus</u>	2	0.00	0.01 NS

**P < 0.001, *P < 0.01, NS = not significant.

S. validus decreased with increasing initial proportions of S. validus (Fig. 5-8).

Feral Hog Disturbance

Percent cover of cutgrass in disturbed plots was significantly less than in undisturbed plots ($t = 11.98$; $P = 0.0001$; $n = 6$; disturbed mean = 5.83, $SE = 6.11$; undisturbed mean = 39.16, $SE = 3.27$). Percent cover of cutgrass decreased significantly as cutgrass was replaced by softstem bulrush or softstem bulrush mixed with spikerush and cattail.

Discussion

Previous experiments (Chapter 3) have demonstrated the contradiction between field distributions of S. validus along a salinity gradient and the responses to this gradient established in greenhouse experiments. Results of these and of present experiments demonstrated that competitive interactions were important in determining the distribution of S. validus, as well as associated plant species, and indicated the changing role of competition in structuring plant communities along an environmental gradient. Results of disturbance experiments indicated feral hog disturbance, combined with higher salinities, had a significant effect on vegetation composition.

Several studies have demonstrated that differential physiological tolerance of plant species along environmental gradients does not alone explain plant species zonation.

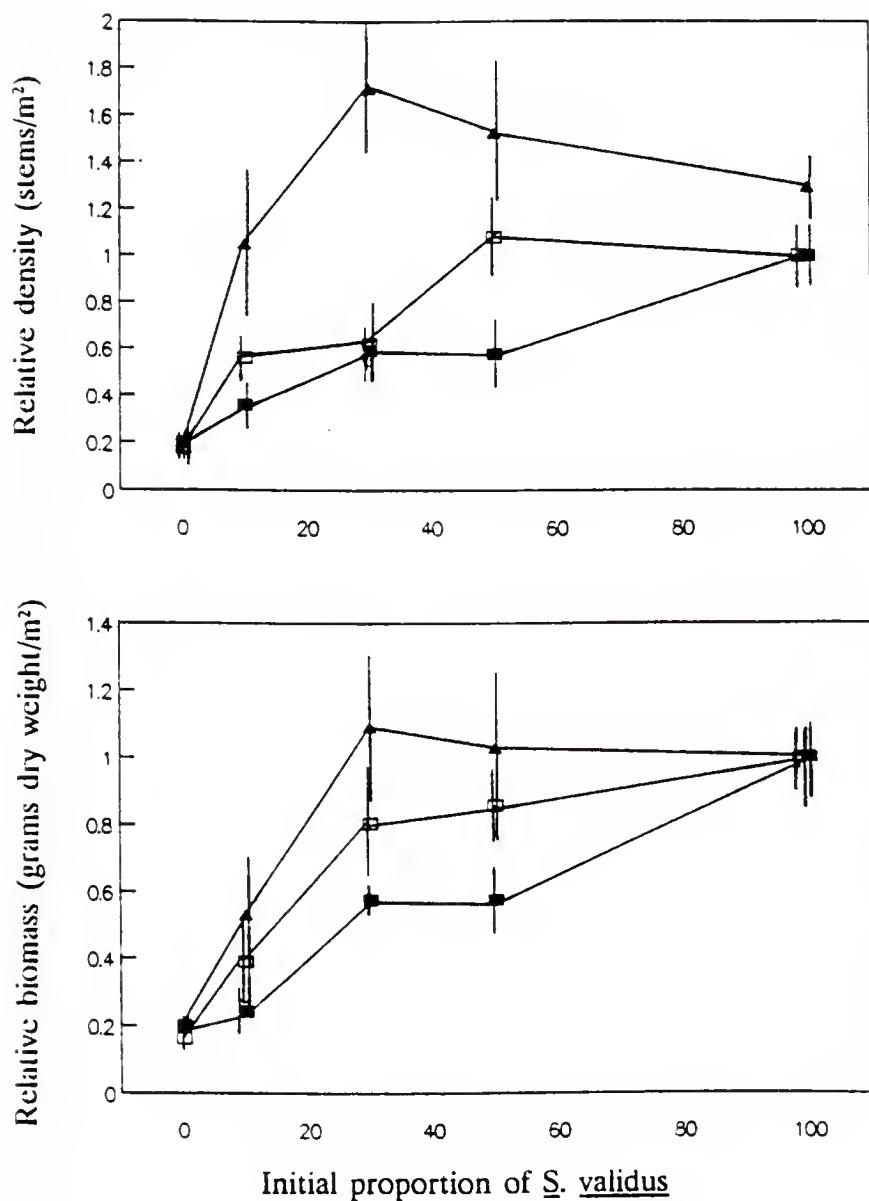


Fig. 5-8. Means and standard errors of total relative yields for density and biomass of all species for different greenhouse soil salinities, plotted against initial density of all species. Solid squares represent freshwater, empty squares represent oligohaline, and solid triangles represent mesohaline soil salinities.

Competitive exclusion across a water depth gradient has been demonstrated for Typha latifolia and T. angustifolia (Grace and Wetzel 1981), in which T. latifolia was physiologically restricted to shallower depths, while T. angustifolia was competitively excluded by T. latifolia to deeper water. Both species, however, grew best at the shallower depth. In addition, Goldberg (1985) found that a tree species characteristic of more favorable soil conditions was restricted from more acid, less fertile soil by physiological intolerance, while the species from the less favorable soil was restricted from the more fertile soil by competition.

Results of the present study were consistent with these findings. Freshwater plant species, predominantly E. montevidensis, Z. miliaceae, Polygonum spp., and Sagittaria spp. were inhibited by increased salinities in greenhouse experiments, and restricted to the freshwater marsh due to salinity intolerance. An ecological generalist, S. validus occurred over a wider range of salinities, but was limited in its competitive abilities. Scirpus validus did poorly when grown with other species under freshwater conditions, both in greenhouse and field experiments, where competitive abilities of freshwater species were greater. Competitive inhibition of S. validus, expressed as its increase when neighbor species were removed, was greater under freshwater and mildly oligohaline conditions when compared with the

mesohaline marsh. These results indicated a significant reduction in biomass and densities of S. validus at the freshwater site in response to the greater competitive abilities of the more specialized freshwater species, even though, experimentally, it exhibits significantly better growth under freshwater conditions. Scirpus validus persisted, however, by colonizing gaps in the vegetation due to disturbance or die-back of other species.

As a generalist species, S. validus was able to take advantage of any available resources, whereas the more specialized, niche-differentiated species require more specific resources. Removal of other species provided gaps in freshwater vegetation that were colonized by the more opportunistic S. validus. Removal of S. validus does not, however, enhance the growth of its neighbors. The neighboring freshwater species, because of their greater specialization, may suffer increased interspecific competition among each other and smaller increases in biomass and density even when gaps are available by the removal of S. validus. If distribution of S. validus was limited solely by dispersal, then transplants of it into freshwater marsh would have been unaffected by freshwater species. Early successional characteristics of S. validus, such as longer internode lengths, earlier seasonal appearance, rapid gap invasion, and a general fugitive behavior (personal observations) may allow it to colonize

open gaps quickly and maintain its presence in the freshwater marsh. All freshwater individuals appeared to be inhibited by the presence of neighbors, and gaps were subsequently colonized by individuals in close proximity to the gaps.

My results provided evidence in support of greater competitive influence on a species' distribution at the more benign end of its environmental tolerance range; the distribution of S. validus in these tidal marshes was determined more by competitive interactions under freshwater conditions, and more by physiological tolerance along the higher salinity portions of the gradient. Although S. validus and S. alterniflora both have low competitive abilities, when they occur together resource requirements overlap and the competitive effect appears to be more intense.

Experiments with early and late successional species have found greater niche and resource overlap among generalist species of early successional plants resulted in relatively more aggressive competition, while late successional species have more finely tuned resource requirements and actually compete less among themselves (Parrish and Bazzaz 1982, Pickett and Bazzaz 1978). Relatively benign conditions of tidal freshwater marshes are characteristic of late successional plant communities comprised of species with high niche differentiation.

Brackish marshes, in contrast, impose a physiological salinity stress on plants, creating a habitat analogous to an early successional stage in which plants share resource requirements and niche overlap is high. In a comparison of tidal freshwater and salt marshes, Odum (1988) also described a greater fundamental niche overlap among salt marsh plants when compared with freshwater species. Greater niche overlap among species of the salt-stressed mesohaline marsh may explain the more conspicuous differences in inner and outer plots following thinning and removal of S. validus or neighbor species. Results from transplant experiments suggest that along a gradient of salinity-imposed stress, competition is more intense among less specialized species of higher salinity marshes where demands for resources overlap and species must compete for the same resources.

Several authors have contended that similar resource requirements of plants for water, light, and carbon dioxide make hypotheses regarding niche overlap and diversification irrelevant to plant community structure (Goldberg and Werner 1983, Huston 1979). Miller and Werner (1987) have established an inverse correlation between competitive effects on species and competitive response of plant species to other species, as well as an absence of differential resource requirements in a first-year old-field community. Miller and Werner found that some species had a large inhibitory effect on inferior competitors, and this effect

was not related to the presence of additional neighboring species. This results in the development of a competitive hierarchy among species, in which species are competitively superior or inferior relative to one another, regardless of whether other species are present. While these studies may be applicable for plant species assemblages within a similar range of environmental conditions, a gradient of freshwater and brackish marshes do not provide the same conditions for all plants, nor do they support the same species assemblages.

For example, competitive effects of a species on neighbors and the response of that species to competitive effects of neighbors were, in this study, inversely related at the freshwater site. Competitive effects of neighbor species on S. validus were significant, while the response of neighbor species to removal of S. validus was insignificant. Under mesohaline conditions, S. validus exhibited no response to S. alterniflora removal, while S. alterniflora did experience a significant increase when S. validus was removed. Within a given set of environmental conditions, then, the present study provides additional evidence in support of the inverse relationship between competitive effect and response suggested by Miller and Werner. These results, by presenting comparisons between low and high salinity marshes, also demonstrate that a single species may have a range of competitive effects and

responses depending on local conditions and co-occurring species.

It might be argued that removal of S. validus results in greater biomass being removed from the mesohaline plots when compared with the freshwater or oligohaline sites since fewer species are present at the mesohaline site and removal of any one species results in the removal of more biomass from a plot. Ostensibly, this could produce what appears to be a strong competitive effect, when in fact the effect would be small if measured on a per-mass basis (Goldberg and Werner 1983). Any species, however, could take advantage of these gaps, especially plants with a rhizome still intact just below the surface. This would result in S. validus recovery in plots where S. validus was removed and S. alterniflora recovery where S. alterniflora was removed. In the freshwater marsh, removal of neighbor species resulted in greater biomass removal because all species except S. validus were removed, and openings were larger than for plots in which only S. validus was removed. Openings again could be colonized by any of the surrounding species. In fact, placement of donor plots of monospecific S. validus in the freshwater marsh provided no available gaps; nonetheless, these plots were immediately invaded and dominated by other freshwater species other than S. validus.

The absence of S. alterniflora and S. robustus at the strongly oligohaline marsh is difficult to explain in terms

of the present salinity regime. Intermediate disturbance hypotheses (Tilman 1982, Huston 1979) proposed that species richness would increase at an intermediate level of disturbance that resulted in greatest spatial and temporal heterogeneity. Recent studies along riverbanks have shown plant species richness to increase at intermediate levels of substrate heterogeneity (Nilsson, 1987). While neither salinity variance nor the variance relative to mean salinity (coefficient of variation) were higher or lower at the strongly oligohaline site, the site is probably undergoing the most recent alteration in salinity due to tidegate operations (see Chapter One), that have resulted in the present gradient of freshwater, oligohaline, and mesohaline tidal marshes along the lower Savannah River. A study of an impounded New England salt marsh showed the previously dominant species, *T. angustifolia*, was replaced by *S. alterniflora* (Sinicrope et al. 1990) following the re-introduction of tidal flushing. This appears to be what is happening at the oligohaline site; while soil salinities are high enough to inhibit freshwater species other than *S. validus*, and *S. alterniflora* does well once established, there has not been time enough for *S. alterniflora* to invade on its own.

Expansion of *S. alterniflora* at the oligohaline site beyond the mesohaline donor transplants as well as into the freshwater donor transplants at the oligohaline site

demonstrated that if salinities were high enough, S. alterniflora, an even greater generalist than S. validus, could successfully become established. S. alterniflora was able to maintain or increase its density and biomass from transplanted plots of S. alterniflora and also invaded transplants of freshwater species at the strongly oligohaline site. The relative abundance of S. alterniflora has been shown to increase following short-term disturbance (Bertness and Ellison 1987) and the disturbance effect of transplanting freshwater plots to the oligohaline site could explain its invasion. Spartina alterniflora did not invade S. validus control plots at the oligohaline site, probably due to the absence of S. alterniflora close enough to S. validus to colonize the controls. My results suggest establishment limits the distribution of S. alterniflora at these increased salinities. The transitional salinities inhibit most freshwater species, but S. validus, which was established prior to the salinity increases, was able to expand its distribution in the absence of competitors. Another salt tolerant species, e.g. S. alterniflora, must first undergo dispersal and establishment, and then compete with and already established species which were able to coexist successfully among highly competitive freshwater species. Spartina alterniflora, like many salt-tolerant species, grows best under freshwater or low salinity conditions (see Chapter 4). Most salt-tolerant species were

out-competed under freshwater conditions, and so were confined to brackish and salt marshes where freshwater species cannot survive (Wainwright 1984, Barbour 1978).

The ability of S. alterniflora to survive at the freshwater site may have been a result of the edging around the transplants, which could have inhibited invasion by some species. Scirpus validus, however, appeared to be the only species substantially inhibited by the rubber edging around transplant plots, most likely a consequence of its rhizome depth. Spartina alterniflora was able to send rhizomes down deep enough to go under edging at mesohaline and oligohaline sites, and E. montevidensis root mats occurred nearly on the marsh surface, enabling it to expand over the edging. Several freshwater species seeded into the plots. Rhizomes of S. validus, however, are intermediate in their depth, and tend to go around or turn in a different direction once they come in contact with tree roots or other plant rhizomes (personal observation).

Invasion of S. validus stands by S. alterniflora was not confined to experimental transplants and may be occurring throughout the mesohaline site. The boundary between stands of S. validus and S. alterniflora, delineated with wooden stakes in 1987, had moved more than a meter into S. validus stands by the end of this study (personal observation). This suggests that the monospecific stands of S. validus in the mesohaline marsh will eventually be

replaced by S. alterniflora and smaller amounts of co-occurring S. validus and S. robustus. Greenhouse results provide little information regarding the ability of S. validus to compete with S. alterniflora at increased salinities other than indicating that factors other than salinity were responsible for increased S. validus at mesohaline field sites when compared with freshwater sites.

The greater yield of freshwater species in greenhouse experiments under freshwater conditions in the absence of S. validus suggested reduced intraspecific interference of freshwater species in species mixtures (Silvertown 1982). Scirpus validus exhibited increases proportional to initial greenhouse densities, indicating no inhibition due to the presence of freshwater species under freshwater conditions. Field experiments, however, indicated a competitive release of S. validus when freshwater species were removed. This suggests that the competitive release was diffuse rather than species-specific, and a result of available gaps in the field experiment once neighbors were removed. In the greenhouse experiments, biomass and density of species other than S. validus did not decrease significantly at higher salinities. Few species, e.g., E. montevidensis, Scirpus robustus, and Leersia virginica remained at the end of the greenhouse experiment. This demonstrated that (1) most species in the freshwater marsh were intolerant of increased salinities, and (2) few species tolerant of increased

salinities were limited by something else in the mesohaline marsh, possibly competition from S. alterniflora and S. validus.

Although S. validus was out-competed in the freshwater marsh by other local species, most of these species were absent from the oligohaline marsh. Zizaniopsis miliacea, T. latifolia, and E. montevidensis remained common, but at the higher salinities did not affect the distribution of S. validus as they did at the freshwater site. Within-site transplants at the mildly oligohaline marsh demonstrated that although S. validus from inner nested plots decreased relative to pure control stands, the change in S. validus density and biomass was least at this site when compared with freshwater and mesohaline sites. Within-site transplants at the mildly oligohaline site exhibited little or no change in S. validus density and biomass for inner S. validus and outer neighbor plots. Very little invasion of transplanted S. validus occurred at this site, suggesting the low salinity marshes inhibit most species, allowing S. validus to expand.

The greater yield of S. validus in freshwater species mixes at oligohaline and mesohaline conditions in both field and greenhouse experiments suggests S. validus had a competitive advantage over surviving freshwater species at higher salinities, although monocultures of S. validus do more poorly at increased salinities.

Decreased re-establishment of neighbor species following experimental removal may also explain the small decrease in S. validus once it was removed from outer neighbor plots at the oligohaline site. Seeds and seedling of plants which generally tolerate low salinities as adults often may be inhibited at the same low salinities (Beare and Zedler 1987, Breen et al. 1977). In addition, disturbance by animals may inhibit re-establishment of species such as Z. miliaceae, T. latifolia, and E. montevidensis and allow a more salt-tolerant species, e.g. S. validus to invade the disturbed sites. It appeared that, once established at these low salinities, S. validus suffered relatively low competitive reduction in biomass and density. Oligohaline marsh conditions may be the transition beyond which most species were intolerant of the increased salinities.

The oligohaline marsh site was strongly affected by disturbance events. In addition, seasonal variation in plant growth, and increased salinities may be as important as actual disturbance by feral hogs. During the growing season feral hogs were observed throughout the area. Rooting disturbances were small (approximately 25 X 25 cm in size, personal observation), dispersed, and frequent (approximately 3 per 10 m², personal observation), and were quickly recolonized by vegetative expansion of surrounding plant species. During winter months hogs generally occurred in larger groups, feeding more heavily on roots and rhizomes

than they do in spring when mast was more available (Wood et al. 1979). Disturbed areas adjacent to levees in the study area were trampled and uprooted, leaving the ground muddy and void of standing vegetation. Plants able to sprout from seeds and rhizomes during winter months, as S. validus does, may recolonize the area at a much greater rate than Z. miliaceae. The broad environmental tolerances of S. validus (Beal 1977, Barko and Smart 1978, Langeland 1981, Joyce and Thayer 1986) are characteristic of early successional species, whereas Z. miliaceae appeared to be a later successional species, exhibiting less tolerance to disturbance and changing salinities.

Increased soil water salinities may exacerbate disturbance effects on vegetation. Combined with bare areas created by the hogs, increased soil salinities may inhibit seedlings and new sprouts of giant cutgrass. Scirpus validus, however, germinated and sprouted from rhizomes under low and brackish interstitial salinities, which may have inhibited colonization by giant cutgrass.

In summary, competitive interactions and their effect on species distributions and associations in tidal marshes were not exclusively related to the individual competitive abilities of plant species, but instead reflected the competitive balance or ratio of the species involved. Species distributions may also be strongly affected by local disturbance due to animals. The indicator species, S.

validus, was a generalist species and a poor competitor. More specialized freshwater species have greater competitive abilities and may actually compete less with each other, although their effect on S. validus, a generalist, was significant. As increasing salinities impose greater physiological stress and species occurrence was limited by physiological tolerance, co-occurring species with similar competitive abilities experienced more intense competitive interactions. As a result, the competitive balance may be reversed: a competitive subordinate in the freshwater marsh becomes a competitive dominant in the brackish marsh. Under a given set of environmental conditions, the effects of competitive interaction resulted in a competitive hierarchy which strongly influenced plant species occurrence and distribution. Over a wide range of environmental conditions, however, a species with wide environmental tolerances may cross over several distinct species assemblages. While the competitive ability of a generalist species itself was not altered, differences in co-occurring species and environmental conditions resulted in altered competitive hierarchies and variation in species distributions along the environmental gradient.

CHAPTER 6
SUMMARY AND CONCLUSIONS

Summary

The 4 marsh study sites varied significantly in regards to plant species composition, soil salinities, soil organic content, and elevation and hydroperiod. Differences in these environmental parameters were more subtle within each site, although some sites exhibited steeper gradients than others. Physical parameters which imposed a relatively steep environmental gradient on plant species were more strongly related to, and had greater effects on, plant species composition and distribution than parameters which exhibited relatively gradual gradients. Salinity changes from tidal freshwater to mesohaline marshes corresponded significantly to changes in marsh species composition, with the freshwater marsh supporting a significantly higher diversity of plant species than more saline sites. Elevation and distance from tidal channels were significant in differentiating among vegetation classes only within a given salinity regime, and overlap between vegetation classes was greater based on these parameters when compared to salinity.

Steepness of environmental gradients, similarity in resource requirements, and differences in scale of

measurement may all influence the extent of overlap among vegetation classes. The extensive habitat overlap of freshwater species was characteristic of a "finer grained" or more homogeneous habitat in which habitat differences, e.g. salinity or elevation, were not discrete at the level measured. In contrast, greater differences in environmental parameters over equal or small distances at oligohaline and mesohaline sites resulted in steeper gradients and can be considered "coarse grained" habitats.

Scirpus validus was the only species which occurred throughout the study area, and exhibited changes in spatial pattern and morphology, both of which were strongly associated with salinity. Pattern differences suggested that processes other than random chance were affecting the distribution of S. validus. Significant differences in morphological variation and associated salinities between greenhouse and field experiments indicated that salinity alone was not responsible for the the variation in field morphology or spatial patterns. Light differences between sites due to variability in vegetation composition and structure suggested that light availability may be an important resource for which species were competing. This resulted in pattern and morphology differences that otherwise appeared related to a strong salinity gradient.

In addition to environmental gradients, feral hog disturbance appeared to significantly affect species

composition at low salinity sites. Disturbed plots underwent changes from Z. miliaceae-dominated vegetation to predominantly S. validus, and indicated feral hog disturbance can exacerbate the change from freshwater to brackish marsh vegetation under the present salinity regime.

While much of the variation in plant species associations and distributions can be attributed to the strong salinity gradient, evidence from chapters two through four showed factors other than physical gradients were also responsible for observed differences in species distributions. Results of competition experiments in Chapter 5 indicated the occurrence of significant interactions among plant species. Results also demonstrated the significant variation in competitive interactions among species and the effects of variation in competitive interactions on plant community structure in freshwater and more saline marshes.

Scirpus validus, a generalist, exhibited a characteristically poor competitive ability in both freshwater and mesohaline marshes, as did Spartina alterniflora, a mesohaline species. Species co-occurring with S. validus in the freshwater marsh exhibited greater competitive abilities characteristic of more specialized, relatively later successional species. As a result, competitive interactions were more balanced and appeared more intense in the higher salinity marshes. The

overall effects on species composition and distributions were, however, more strongly influenced by competition in the freshwater marsh, where species' competitive abilities were more varied.

Conclusions

Several authors have suggested that plant species zonation and distributions are attributable to differential competitive abilities along an environmental gradient, while few have experimentally shown variations in competitive abilities for different species along such a gradient (see Chapters 1 and 5). Unlike the former, in which differences in species distributions were noted and competition was suggested as a possible mechanism, this study first determined whether or not competition was actually occurring. While the latter experiments have shown differential competitive abilities for pair-wise combinations of species, the relative aggressiveness of species in mixtures and subsequent effects on dominance hierarchies have not been addressed. Results of this study not only confirm recent work by providing additional evidence of differential competitive abilities along environmental gradients, but add to the current understanding by addressing the effects of competitive interactions and environmental influences on plant community structure.

Plant species composition and distributions across the

strong salinity gradient of tidal freshwater and brackish marshes were most likely determined by species' salinity tolerances. Within a given salinity regime, however, competitive interactions had a significant influence upon plant species distributions. Competitive interactions and their effect on species distributions and associations were not exclusively related to the individual competitive abilities of plant species, but instead reflected the competitive balance or ratio of the species involved.

As increasing salinities imposed greater physiological stress and species occurrence was limited by physiological tolerance, co-occurring species with similar competitive abilities experienced more intense competitive interactions. As a result, the competitive balance may be reversed: a competitive subordinate of the freshwater marsh becomes a competitive dominant in the brackish marsh. Under a given set of environmental conditions, the effects of competitive interaction resulted in a competitive hierarchy which strongly influenced plant species occurrence and distribution. Over a wide range of environmental conditions, however, a species with wide environmental tolerances may cross over several distinct species assemblages. While the competitive ability of a generalist species itself was not altered, its relative competitive ability compared with co-occurring species under different environmental conditions resulted in altered competitive

environmental conditions resulted in altered competitive hierarchies and variation in species distributions along an environmental gradient.

The role of competition in structuring plant species assemblages across the salinity gradient on the lower Savannah River was significant. Species competitive interactions are not, however, more "important" in one community than another. Competition is not a function of absolute competitive ability or salinity stress, but does reflect the competitive balance of competing individuals under a given set of environmental conditions. Competition among plant species in the environmentally benign freshwater marsh reflected greater, more complex niche differentiation, with distinct differences in competitive ability, and resulted in less intense, more diffuse, competition among several species. The salinity-stressed mesohaline marsh supported fewer species with relatively similar resource requirements, resulting in more intense competition for the same resources.

LITERATURE CITED

Afifi, A. A. and V. Clark. 1984. Computer-aided multivariate analysis. Wadsworth, Inc., London, England.

Adams, D. A. 1963. Factors influencing the vascular plant zonation in North Carolina salt marshes. *Ecology* **44**:445-455.

Anderson, D. J. 1986. Ecological succession. p. 269-285. In J. Kikkawa and D.J. Anderson, editors. *Community Ecology: Pattern and Process*. Blackwell Scientific Publications, London, England.

Baden, J. III., W. T. Batson, and R. Stalter. 1975. Factors affecting the distribution of vegetation of abandoned rice fields, Georgetown Co., South Carolina. *Castanea* **40**:171-181.

Bakker, J. P. 1985. The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio* **62**:391-398.

Barbour, M. G. 1978. The effect of competition and salinity on the growth of a salt marsh plant species. *Oecologia* **37**:93-99.

Barclay, A. M. and R. M. M. Crawford. 1982. Plant growth and survival under strict anaerobiosis. *Journal of Experimental Botany*. **33**:541-549.

Barko, J. W. and R. M. Smart. 1978. The growth and biomass distribution of two emergent freshwater plants, *Cyperus esculentus* and *Scirpus validus*, on different sediments. *Aquatic Botany* **5**:109-117.

Barko, J. W. and R. M. Smart. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. *Ecological Monographs* **51**:219-235.

Barko, J. W., D. G. Hardin, and M. S. Mathews. 1982. Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. *Canadian Journal of Botany* **60**:877-887.

Beal, E. O. 1977. A manual of marsh and aquatic plants of North Carolina. Technical Bulletin no. 247. North Carolina Agricultural Experimental Station. Raleigh, North Carolina, USA.

Beals, E. W. 1969. Vegetational change along altitudinal gradients. *Science*. **165**:981-985.

Beare, P. A., and J. B. Zedler. 1987. Cattail invasion and persistence in a coastal salt marsh: the role of salinity reduction. *Estuaries* **10**:165-170.

Bernard, J. M., F. K. Seischab, and H. G. Gauch, Jr. 1983. Gradient analysis of the vegetation of the Byron-Bergen swamp, a rich fen in western New York. *Vegetatio* **53**:85-91.

Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs* **57**:129-147.

Bratton, S. P. 1974. The effect of the European Wild Boar (*Sus scrofa*) on the high-elevation vernal flora in Great Smoky Mountains National Park. *Journal of the Torrey Botanical Club* **4**:198-206.

Breen, C. M., C. Everson, and K. Rodgers. 1977. Ecological studies on *Sporobolus virginicus* (L.) Kunth. with particular reference to salinity and inundation. *Hydrobiologia* **54**:135-140.

Brown, J. D., E. M. EuDaly and J. P. Davis. 1987. An innovative analysis of port development impacts on a coastal national wildlife refuge. Pages 2269-2281 in Coastal zone '87: Proc. of the sixth symposium on coastal and ocean management. Seattle, Washington, USA.

Chabreck, R. H. 1968. The relation of cattle and cattle grazing to marsh wildlife and plants in Louisiana. *Proceedings of the Annual Conference of the Southeast Association of the Game and Fish Commission*. **22**:55-58.

Clausen, J. D., D. Keck, and W. M. Hiesey. 1948. Experimental studies on the nature of the species. III. Environmental responses of climatic races of *Achillea*. Carnegie Inst. Washington Publ. No. 581.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**:566-576.

Cooper, A. 1982. The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. *New Phytologist* **90**:263-275.

Dale, M. R. T. 1986. Overlap and spacing of species along an environmental gradient. *Oikos* **47**:303-308.

Davidson, D. W. 1978. Size variability in the worker caste of a social insect (*Veromessor pergandei mayr*) as a function of the competitive environment. *American Naturalist* **112**:523-532.

Dawe, N. K., and E. R. White. 1982. Some aspects of the vegetative ecology of the Little Qualicum River estuary, British Columbia. *Canadian Journal of Botany* **60**:1-447-1459.

de la Cruz, A. A. 1981. Differences between South Atlantic and Gulf Coast marshes. In R. Carey, P. S. Markovits, and J. B. Kirkwood, editors. *Proceedings U.S. Fish and Wildlife Service Workshop on Coastal Ecosystems of the Southeastern United States*. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-80/59.

Disraeli, D. J., and R. W. Fonda. 1979. Gradient analysis of the vegetation in a brackish marsh in Bellingham, Washington. *Canadian Journal of Botany* **57**:465-475.

Donovan, L. A. and J. L. Gallagher. 1985. Morphological responses of a marsh grass, *Sporobolus virginicus* (L.) Kunth., to saline and anaerobic stresses. *Wetlands* **5**:1-13.

Ellison, A. M. 1987. Density-dependent dynamics of *Salicornia europaea* monocultures. *Ecology* **68**:737-741.

Ewing, K. 1983. Environmental controls in Pacific Northwest intertidal marsh plant communities. *Canadian Journal of Botany* **61**:1105-1116.

Ferren, W. R. 1976. Aspects of the intertidal zones, vegetation and flora of the Maurice River system, New Jersey. *Bartonia* **44**:58-67.

Ferren, W. R. Jr. and A. E. Schuler. 1980. Intertidal vascular plants of river systems near Philadelphia. *Proceedings of the Academy of Natural Sciences and Philosophy* **132**: 86-120.

Fowler, N. and J. Antonovics. 1981. Competition and coexistence in a North Carolina grassland: I. Patterns in undisturbed vegetation. *Journal of Ecology* **69**:825-841.

Gambrell, R. P. and W. H. Patrick Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. pp. 375-423 In D. D. Hook and R. M. M. Crawford, editors. *Plant life in Anaerobic Environments*. Ann Arbor Scientific Publications, Ann Arbor, Michigan, USA.

Godfrey, R. K. and J. W. Wooten. 1979. *Aquatic and wetland plants of the southeastern United States: Monocotyledons*. University of Georgia Press, Athens, Georgia, USA. 712 p.

Goldberg, D. E. 1985. Effects of soil pH, competition, and seed predation on the distributions of two tree species. *Ecology* **66**:503-511.

Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *American Journal of Botany* **70**:1098-1104.

Gosselink, J. G. and R. E. Turner. 1978. The role of hydrology in freshwater wetland ecosystems. pp. 63-78 In R.E. Good, D.F. Whigham and R.L. Simpson, editors. *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press, New York, New York, USA.

Grace, J. B. and R. Wetzel. 1981. Habitat positioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist* **113**:463-474.

Haramis, G. M., and V. Carter. 1983. Distribution of submerged aquatic macrophytes in the tidal Potomac River. *Aquatic Botany* **15**:65-79.

Heinselman, M. L. 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. *Ecological Monographs* **40**:235-261.

Hill, M. O. 1979. DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, New York, USA.

Hoover, J. K. 1984. Spatial and temporal niche relationships in a tidal freshwater macrophyte community. MS Thesis. University Virginia, Charlottesville, Virginia, USA.

Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81-101.

Jackson, C. R. 1952. Some topographic and edaphic factors affecting plant distribution in a tidal marsh. *Quarterly Journal of the Florida Academy of Sciences* **15**:137-146.

Jefferies, R. L. 1981. Osmotic adjustment and responses of halophytic plants to salinity. *Bioscience* **31**:42-46.

Jones, H. G. 1983. Plants and microclimate: a quantitative approach to environmental plant physiology. Cambridge University Press, New York, USA.

Joyce, J. C. and D. D. Thayer. 1986. Evaluation of the potential impact of herbicides used for water hyacinth control on bulrush communities. *In Annual Report USDA/ARS-IFAS/Univ of Florida Cooperative Agreement*. Gainesville, Florida, USA.

Kershaw, K. A. 1973. Quantitative and dynamic plant ecology. American Elsevier Publishing Co., New York, New York, USA.

King, T. J. and S. R. J. Woodell. 1973. The causes of regular pattern in desert perennials. *Journal of Ecology* **61**:761-765.

Kirby, C. J., and J. G. Gosselink. 1976. Primary production in a Louisiana gulfcoast Spartina alterniflora marsh. *Ecology* **57**:1052-1059.

Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology* **70**:36-47.

Kolasa, J., and D. Strayer. 1988. Patterns of the abundance of species: a comparison of two hierarchical models. *Oikos* **53**:235-241.

Kruczynski, W. L., C. B. Subrahmanyam, and S. H. Drake. 1978. Studies on the plant community of a north Florida salt marsh. Part I. Primary production. *Bulletin of Marine Science* **28**:316-334.

Langeland, K. 1981. Bulrush-Scirpus spp. *Aquatics* 3:4,15.

Leck, M. A. and K. J. Graveline. 1979. The seedbank of a freshwater tidal marsh. *American Journal of Botany* 66(9):1006-1015.

Lieffers, V. J. 1983. Emergent plant communities of oxbow lakes in NE Alberta: salinity, water level fluctuations and succession. *Canadian Journal of Botany* 62:310-316.

Lister, B. C. 1976a. The nature of niche expansion in West Indian Anolis lizards. I. Ecological consequences of reduced competition. *Evolution* 30:659-676.

Mack, R. N. and J. L. Harper. 1977. Interference biennials: spatial pattern and neighborhood effects. *Journal of Ecology* 65:345-64.

Mathews, T. D., F. W. Stapor, C. R. Richter, J.V. Miglarese, M. D. McKenzie, and L.A. Barclay. 1980. Ecological characterization of the sea island coastal region of South Carolina Georgia. U.S. Fish Wildl. Serv. Biol. Serv. Program, Washington, D.C. FWS/OBS-79/40.

McMillan, C. 1959. Salt tolerance within a Typha population. *American Journal of Botany* 521-526.

McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. *Science* 167:131-139.

McNeely, D. L. 1987. Niche relations within an Ozark stream cyprinid assemblage. *Environmental Biology of Fishes* 18:195-208.

Miller, T. E. and P. A. Werner. 1987. Competitive effects and responses between plant species in a first-year old-field community. *Ecology* 68:1201-1210.

Mitsch, W. J. and J. G. Gosselink. 1986. *Wetlands*. Van Nostrand Reinhold Company, New York, New York, USA.

Mooring, M. T., A. W. Cooper, and E. D. Seneca. 1971. Seed germination response and evidence for height ecophenes in Spartina alterniflora from North Carolina. *American Journal of Botany* 58:48-55.

Morris, A. W., A. J. Bale, and R. J. M. Howland. 1978. Very low salinity regions of estuaries: important sites for chemical and biological reactions. *Nature* 274:678-680.

Nilsson, C. 1987. Distribution of stream-edge vegetation along a gradient of current velocity. *Journal of Ecology* 75:513-522.

Nilsson, C., G. Grelsson, M. Johansson, and U. Sperens. 1989. Patterns of plant species richness along riverbanks. *Ecology* 70:77-84.

Odum, E. P., J. L. Cooley, J. B. Birch, J. E. Irwin, A. H. Roberts, G. G. Perlmutter, and J. Powers. 1977. Ecological inventory and waste management assessment of BASF Wyandotte Corporation property, Chatham county, Georgia. Second Annual Progress Report, Volume II, pp. 5-19. University of Georgia, Athens, Georgia, USA.

Odum, W. E. 1988. Comparative ecology of tidal freshwater and salt marshes. *Annual Review of Ecological Systems* 19:147-176.

Odum, W.E., M.L. Dunn, and T.J. Smith III. 1978. Wetland function and values: the state of our understanding. American Water Resource Association. TPS 79-2.

Odum, W. E., T. J. Smith III, J. K. Hoover, and C. C. McIvor. 1984. The ecology of tidal freshwater marshes of the United States east coast: a community profile. U.S. Fish and Wild. Serv. FWS/OBS-83/17.

Parrish, J. A. D., and F. A. Bazzaz. 1982. Competitive interactions in plant communities of different successional ages. *Ecology* 63:314-320.

Parrondo, R. T., J. G. Gosselink, and C. S. Hopkinson. 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. *Botanical Gazette* 139:102-107.

Pearlstine, L., R. Bartleson, W. Kitchens, and P. Latham. 1989. Lower Savannah River hydrological characterization. Technical report no. 35. School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA.

Pezeshki, S. R., R. D. Delaune, and W. H. Patrick, Jr. 1987. Response of baldcypress (*Taxodium distichum* L. var. *distichum*) to increases in flooding salinity in Louisiana's Mississippi River deltaic plain. *Wetlands* 7:1-10.

Phleger, C. F. 1971. Effect of salinity on growth of a salt marsh grass. *Ecology* 52:908-911.

Pianka, E. R. 1978. Evolutionary ecology. Harper and Row, New York, New York, USA. 397 pp.

Pickett, S. T. A. and F. A. Bazzaz. 1978. Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology* 56:35-49.

Pielou, E. C., and R. D. Routledge. 1976. Salt marsh vegetation: latitudinal gradients in the zonation patterns. *Oecologia* 24:311-321.

Pielou, E. C. 1959. The use of point-to-plant distances in the study of the pattern of plant populations. *Journal of Ecology* 47:607-613.

Platt, W. J., and M. I. Weis. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. *The American Naturalist*. 111:479-513.

Ponnamperuma, F. N. 1972. The chemistry of submerged soils. *Advances in Agronomy* 24:29-96.

Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* 29:254-283.

Rabinowitz, D. S. 1978. Early growth of mangrove seedlings in Panama, and a hypothesis concerning the relationship of dispersal and zonation. *Journal of Biogeography* 5:113-133.

Rhodes, R. F. 1949. The hydraulics of a tidal river as illustrated by Savannah Harbor, Georgia. Department of the Army Corps of Engineers, Savannah District, Savannah, Georgia.

Reid, G. K. and R. D. Wood. 1976. *Ecology of Inland Waterways and Estuaries*. D. Van Nostrand Co., New York, New York, USA.

Rowell, D. L. 1981. Oxidation and Reduction. Pages 401-461 In D.J. Greenland and M.H.B. Hayes, editors. *The chemistry of Soil Processes*. John Wiley and Sons, New York, New York, USA.

Seliskar, D. M. 1985. Effect of reciprocal transplanting between extremes of plant zones on morphometric plasticity of five plant species in an Oregon salt marsh. *Canadian Journal of Botany* 63:2254-2262.

Seneca, E. D. 1972. Germination and seedling response of Atlantic and Gulf coast populations of Uniola paniculata. American Journal of Botany **59**:290-296.

Shaltout H. 1987. Pattern, phenology and sex ratio of Egyptian Thymelaea hirsuta populations. Vegetatio **72**:67-73.

Sharitz, R. R. and J. F. McCormick. 1973. Population dynamics of two competing annual plant species. Ecology **54**:723-740.

Shea, M. L., R. S. Warren, and W. A. Neiring. 1975. Biochemical and transplantation studies of the growth form of Spartina alterniflora on Connecticut salt marshes. Ecology **56**: 461-466.

Silvertown, J. W. 1982. Introduction to plant population ecology. Longman Group Limited, New York, New York, USA.

Simpson, R. L., R. E. Good, M. A. Leck, and D. Whigham. 1983. The ecology of freshwater tidal wetlands. Bioscience **33**:255-259.

Sinicroppe, T. L., P. G. Hine, R. S. Warren, and W. A. Neiring. 1990. Restoration of an impounded salt marsh in New England. Estuaries **13**(1):25-30.

Snedaker, S.C. 1982. Mangrove species zonation: why? Pages 111-125 In D. N. Sen and K. S. Rajpurohit, editors. Tasks for Vegetation Science, Vol. 2. W. Junk Publishers, The Hague, Netherlands.

Snow, A. A. and S. W. Vince. 1984. Plant zonation in an Alaskan salt marsh II. An experimental study of the role of edaphic conditions. Journal of Ecology **72**:669-684.

Spence, D. H. N. and H. M. Dale. 1978. Variations in the shallow water form of Potamogeton richardsonii induced by some environmental factors. Freshwater Biology **8**:251-268.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W.H. Freeman and Company, New York, New York, USA.

Taylor, L. R., I. P. Woiwood, and J. N. Perry. 1978. The density-dependence of spatial behaviour and the rarity of randomness. Journal of Animal Ecology **47**:383-406.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Turner, R. E. 1976. Geographic variation in macrophyte production: a review. Contributions in Marine Science 20:48-68.

Turner, M. G. 1987. Effects of grazing by feral horses, clipping, trampling, and burning on a Georgia salt marsh. Estuaries 10:54-60.

Ungar, I. A. 1962. Influence of salinity on seed germination in succulent halophytes. Ecology 43:763-764.

Valiela, I., J. M. Teal, S. Volkman, D. Shafer and E. J. Carpenter. 1978. Nutrient and particulate fluxes in a saltmarsh ecosystem: tidal exchanges and inputs by precipitation and groundwater. Limnology and Oceanography 23:798-812.

Van Valen, L. 1965. Morphological variation and width of ecological niche. American Naturalist 99:377-390.

Vince, S.W. and A. Snow. 1984. Plant zonation in an Alaskan salt marsh. I. Distribution, abundance, and environmental factors. Journal of Ecology 72:651-667.

Wainwright, S. J. 1984. Adaptations of plants to flooding with salt water. In T. T. Kozlowski, editors. Flooding and Plant Growth. Academic Press, New York, New York, USA.

Watson, P. J. and J. L. Fyfe. 1975. Potentilla erecta in two contrasting habitats-- a multivariate approach. Heredity 34:417-422.

Webb, K. W. 1966. NaCl effects on growth and transpiration in Salicornia bigelovii, a salt marsh halophyte. Plant and Soil, 24:230-242.

Wharton, C. H., W. M. Kitchens, E. C. Pendleton, and T. W. Sipe. 1982. The ecology of bottomland hardwood swamps of the Southeast: a community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D. C., U.S.A. FWS/OBS-81/37.

Wharton, C. H. 1978. The natural environments of Georgia. Geologic and Water REsources Division and Resource Planning Section, Office of Planning and Research,

Georgia Department of Natural Resources, Atlanta,
Georgia, USA.

White, D. A. 1983. Plant communities of the lower Pearl
River basin. *The American Midland Naturalist*
110:381-345.

Whittaker. R. H. 1965. Dominance and diversity in land
plant communities. *Science* **147**:250-260.

Whittaker R. H. 1975. Communities and ecosystems.
Macmillan Publishing Co., New York, New York, USA.

Wilson, S. D. and P. A. Keddy. 1986. Species competitive
ability and position along a natural stress/disturbance
gradient. *Ecology* **67**:1236-1242.

Wood, G. W. and R. H. Barrett. 1979. Status of wild pigs
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246.

Biographical Sketch

Pamela Jean Latham was born 23 December, 1955, at Parris Island Marine Corps Base, South Carolina, to Robert H. and Jean B. Latham. After travelling extensively throughout the United States, the family settled in Maitland, Florida in 1969. Pam graduated from Lyman High School, Longwood, Florida in 1974 and received her Bachelor of Science degree in Biology from the University of Central Florida, Orlando, Florida, in 1979.

Pam taught high school chemistry and biology in the Seminole County School system from 1979 through 1984 while working towards a Master's Degree in Biological Science. Her Master's thesis was titled "Structural Comparisons of Sand Pine Scrubs of East-Central Florida", and was the first quantitative analysis of Florida's endemic Sand Pine Scrubs. Pam received the degree of Master of Science in 1985, also from the University of Central Florida.

Later in 1985, Pam enrolled in the Ph.D. program in Systems Ecology, in the College of Environmental Engineering Sciences, at the University of Florida, Gainesville, Florida. She married Clay Phillips, a fellow Lyman High School Alumnus in 1986 and in June, 1990, Latham Kathleen Phillips was born. In August, 1990, Pam received her Ph.D., and hopes to continue to work in ecosystems research and possibly begin teaching again.

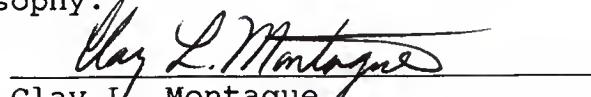
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Wiley M. Kitchens
Wiley M. Kitchens, Chairperson
Professor of Environmental
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